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A Monograph of the Nearctic Plagiochilaceae

Part II. Sectio Zonatae through Sectio Parallelae.*

RUDOLF M. SCHUSTER

Duke University, Durham, N.C.[1]

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Sectio II. ZONATAE Carl, emend. Schuster

Plants moderate in size (their leaves usually 1-2.6 mm long), *olive-tinged to brownish, the stems deep brown, shining when dry, usually dense-leaved,* the aerial shoots slender, elongate, *unbranched or rarely monopodially branched, the branches all intercalary.* Stem with cortex 3-stratose, well-developed for the size of the plant; *cortical cells only* 2-3 × *as long as wide.* Leaves *strongly postically secund, suborbicular to broadly ovate-triangular, ca.* 0.9-1.4 × as long as wide,

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* Part I. Introduction and Sectio I. Asplenioides appeared in THE AMERICAN MIDLAND NATURALIST 62(1):1-166. References will be included in the terminal part.

[1] Present address: University of Massachusetts, Amherst, Mass.

ampliate, widest just above base, their margins armed with relatively numerous (usually 15-50) sharp, spinose teeth; leaves short-decurrent postically, but long-decurrent antically, the straight or somewhat convex antical margin very strongly recurved, *often tubularly so for the whole length of the leaf,* frequently so strongly that it is almost impossible to flatten the leaf. *Leaf-cells relatively small* (*ca.* 12-20 μ wide in leaf apex and 14-24 μ in the leaf middle), *at base forming a distinct but not sharply defined median vitta* of pronouncedly elongate cells (*ca.* 14-23 x 40-72 μ); cells $\pm$ *strongly collenchymatous,* often with bulging trigones (produced even under exceedingly humid and shaded conditions) but with the marginal 1-3 cell-rows tending to be strongly equally thick-walled; oil-bodies (in known species) *glistening, smooth,* nearly or quite *homogeneous,* or (*P. semidecurrens*) very faintly granular-appearing, under oil-immersion.

Reproduction entirely by sexual means: *caducous leaves and leafy propagula constantly lacking. Perianth relatively elongate* (length of dorsal and ventral keels subequal, *ca.* 2-3 times the width of the nearly squarely truncate or somewhat rounded, copiously ciliate to dentate mouth), the keels winged or wingless. Gynoecia situated at the apices of leading shoots, normally with 1-2 innovations; if with 2 innovations the shoot system becoming superficially dichotomous (the innovations then usually remaining sterile), if with 1 innovation the gynoecia becoming pseudolateral (the innovation then often again fertile). *Androecia solitary,* intercalary, compact, spike-like, formed of (4) 6-10 pairs of closely imbricated bracts.

Branching in the Zonatae has been investigated in detail in *P. sharpii sharpii,* in copious material from the Chattooga Narrows, N.C. (*Schuster* 39410). The branches, as in the Sectio Asplenioides, are exclusively intercalary. The branching patterns exhibited are of considerable systematic significance, since they suggest similarities to *Chiastocaulon* Carl. In *P. sharpii* the primary aerial shoots frequently produce a positively phototropic branch, initially spreading at right angles but almost immediately geniculate and coming to lie parallel to the parent shoot; this branch and the parent shoot are rhizoid free. This branch, at or near the point of angulation, gives rise to a negatively phototropic small-leaved, flagelliform stoloniferous branch that bears only rudimentary leaves but freely produces rhizoids. Similar branching occurs in the Sectio Asplenioides (see Fig. 10B:2), the opposite-leaved species of *Plagiochila* now assigned to *Plagiochilion,* and possibly elsewhere in the complex of taxa which are primitive in lacking propagula, in having unspecialized perianths, etc. Unlike in *Plagiochilion,* where a similar mode of branching occurs, the rhizoids are scattered — some arising from near the bases of the vestigial leaves, others from the ventral stem surface. Although the positively phototropic primary branch is lateral in origin, and arises from the ventral portion of a leaf axil, the secondary, flagelliform branch appears postical in origin; it is also intercalary. Infrequently the initial branch developing from a leafy shoot is small-leaved, stoloniferous, rhizoidous

and negatively phototropic. The chief differences between branching in the Zonatae, and in *Chiastocaulon,* lie in (a) the lateral, rather than postical origin of the intercalary leafy branches; (b) the absence of terminal branches from the leading axes.

P. sharpii, when with unfertilized perianths, also shows intercalary innovations. Usually two of these arise, sometimes both from below the perichaetial bracts. However, it is not rare to find the unusual situation arising where an innovation arises immediately below the archegonia, from the shoot tip *within* the perianth. Not infrequently one innovation, of a pair, originates between perianth and bract, *i.e.,* in the axil of the bract, while the other originates below the bract, *i.e.,* in the axil of the leaf subtending the bract. *P. semidecurrens grossidens* also normally develops 1-2 subfloral innovations. Possibly, the regular, if not invariable, development of 1-2 innovations should be regarded as a group character of the Zonatae.

This section is sharply isolated from all our others in the possession of a distinct basal vitta of elongate cells. The elongate perianths and form of the androecia are very similar to those of Sectio Asplenioides, as are the basic leaf-form, the exclusively intercalary branching, the short cortical cells, and the tendency to produce rather numerous marginal teeth of the leaves. However, the nearly or quite homogeneous oil-bodies, the generally coarser teeth of the leaves, the more strongly collenchymatous cells (under equal moisture conditions), as well as the basal vitta set this section sharply off from Sectio Asplenioides.

The homogeneous oil-bodies are shared with Sectio Bidentes, but this section differs at once in consisting of delicate plants which do not reproduce sexually, but by means of caducous leaves and leaf-lobes; these plants also have larger cells, and lack the basal vitta.

The two nearctic members of this section are distantly allied to the European *P. spinulosa,* in which the basal vitta is not or less distinct; the marginal cells usually not thick-walled, the median cells larger and *ca.* 25-28 μ, and the cuticle distinctly verruculose; the spinose marginal teeth more elongate and narrow — with the distal 1-2 cells often 2.5-4 $\times$ as long as wide. In *P. spinulosa* the cells possess mostly 4-6 ellipsoidal to fusiform, essentially homogeneous oil-bodies; with age these are occasionally weakly transversely barred and appear faintly "broken" into irregular segments. The oil-bodies average larger (3 x 6 μ to 4 x 7.8-8.5 μ to 3.5-4 x 10-12 μ), and fewer than in *P. sharpii.* Since they are homogeneous, a relationship of the species to the Sectio Zonatae is clear, if distant. In the larger cells (averaging over 25 μ), and lack of a border, *P. spinulosa* approaches the Sectio Bidentes (from which it differs in the more robust size, the form and dentition of the leaves) and the Sectio Choachinae. In some respects, the species stands between these two groups, and might be considered to be a member of a separate Sectio. *P. punctata,* which is related to *P. spinulosa,* is placed both by Carl and myself in the Choachinae. It is possible that *P. spinulosa* should be placed there also.

Our taxa appear to be related more closely to the Himalayan and Japanese species, *Plagiochila semidecurrens* Lehm. and Lindenb. (*in* Lindenberg and Gottsche, Spec. Hep. 142, 1840-44). The exceeding-

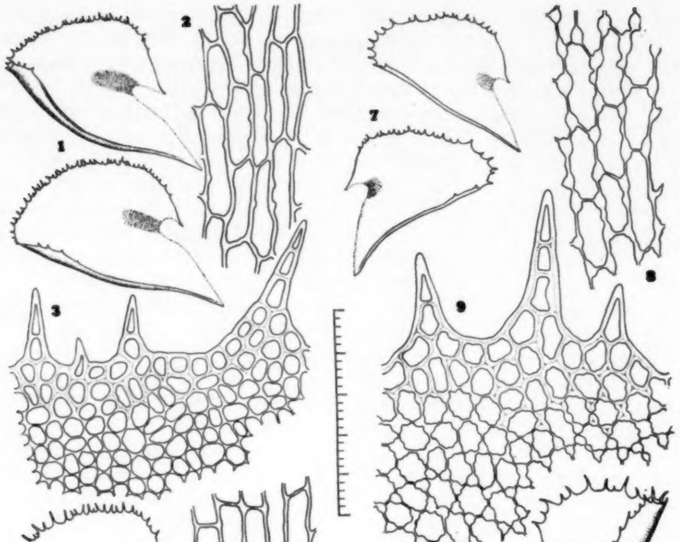

Fig. 15.—Sectio Zonatae: the *Plagiochila semidecurrens-sharpii* complex. 1-3. *P. semidecurrens semidecurrens.* 4-6. *P. semidecurrens grossidens.* 7-9. *P. sharpii sharpii.* 10-12. *P. sharpii yakusimensis.* Figs. 1, 4, 7, 10 all leaves (x 12.) (vertical scale, each division 100 μ); figs. 2, 5, 8, 11 all cells of vitta, and figs. 3, 6, 9, 12 all cells of leaf-apices; all x 205 (horizontal scale, each division 10 μ). (Figs. 1-3 from Verdoorn's Hep. Select. et Crit. No. 533, Sikkim-Himalaya; 4-6, type from Verdoorn's Hep. Select. et Crit. No. 544, Japan; 7-9, from type of *P. sharpii;* 10-12, from Hattori's Hep. Jap. No. 180, as "*P. semidecurrens* var. *grossidens.*")

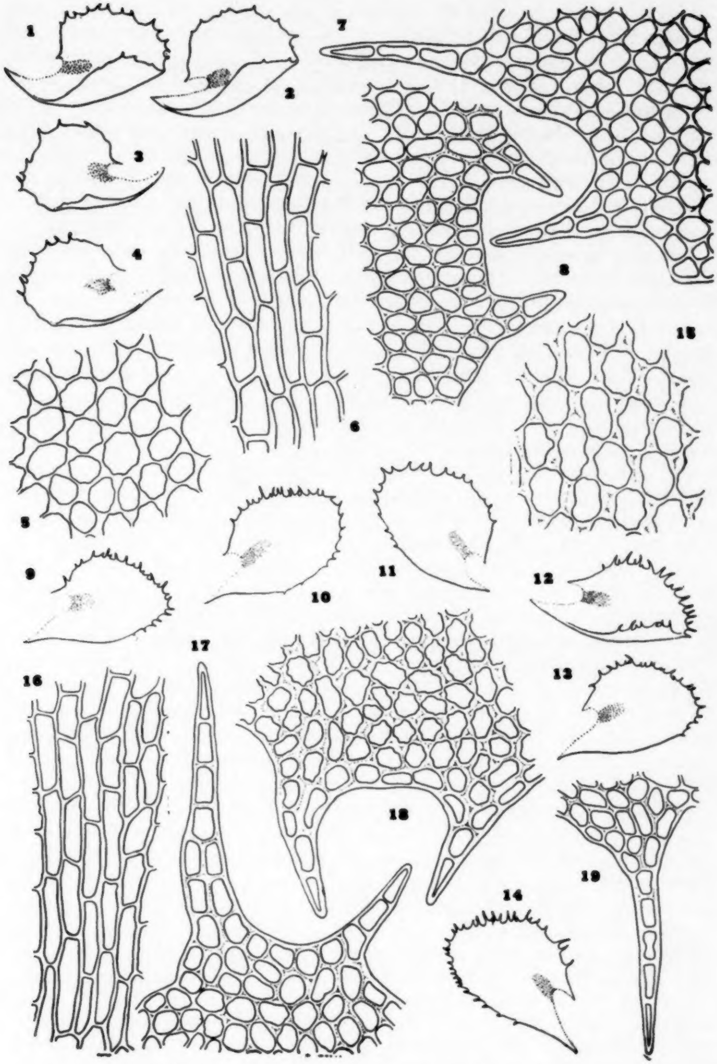

Fig. 16.—*Plagiochila semidecurrens* subsp. *grossidens* (Herz.) Schuster. 1-8 fo. *parva* Hattori (= *P. fryei* Evs., type). 1-4. Leaves; 5. Median cells; 6. Cells of vitta; 7-8. Apical cells and teeth. 9-19. Fo. *alaskana* (Evs.) Schuster (= *P. alaskana* Evs., type). 9-14. Leaves; 15. Median cells; 16. Cells of vitta; 17-18. Cells of leaf apex and apical teeth; 19. Large tooth from posterior margin. (1-4, 9-14, x 12.1; 5-8, 15-19, x 205; drawn to corresponding scale in Fig. 15.)

ly close relationship to *P. semidecurrens* and several other Asiatic species is obscured by Carl's division of the genus into Paleotropic and Neotropic sections, which are supposedly not or only distantly allied to each other. However, Carl (*loc. cit.*, p. 97) admits that in the postically secund leaves the Paleotropic Sectio Zonatae approaches the Neotropic Sectio Arrectae. The Zonatae supposedly differ from the latter group in the small cells ("auffallend dicht"), with the apical cells "höchstens 15 x 15 μ . . . dickwandig und lassen in den Ecken Verdickungen nur undeutlich erkennen." Both groups admittedly share the sharp tendency towards production of a basal vitta.

It should be stressed that the differences in cell-type emphasized by Carl are less evident than he supposes. Although in *P. zonata* Steph., Carl illustrates the cells as equally thick-walled, this does not hold for some of the species he places in the Zonatae. For instance, the first species, *P. semidecurrens* Lehm. and Lindenb., although with equally thick-walled marginal and small (12-14 x 14-16 μ) apical cells, may have nodular trigones. In the tendency for apical and marginal cells to be equally thick-walled, in contrast to the strongly collenchymatous median cells, and in the elongate basal cells, *P. sharpii* and "*P. alaskana*" are exceedingly close to *P. semidecurrens*. Furthermore, in leaf-shape and disposition, *P. sharpii* and "*alaskana*" approach the Zonatae.

For this reason, the writer is of the opinion that the North American species, *i.e.*, "*P. alaskana*" and *P. sharpii* should be referred to the Zonatae. In the strongly collenchymatous cells, and in their larger size (18-20 μ in the leaf apices, rarely barely larger), *P. sharpii* clearly approaches the related paleotropic Sectio Renitentes of Carl (1931). It is perhaps doubtful whether cell size alone will suffice to maintain this section as distinct from the Zonatae. Carl admits that the tendency towards formation of a vitta is characteristic of the Renitentes, as well as the Zonatae, suggesting a direct relationship of the two groups. The tendency for some of the members of both of these groups to freely produce rhizoids from the almost unbranched, slender, aerial leafy shoots is further suggestive of a common origin.

With the relegation of the Appalachian *P. sharpii*, and the Alaskan "*P. alaskana*" and "*P. fryei*" to the Zonatae, the problem arises as to the relationships of these taxa to the Asiatic species of the Zonatae. Such a relationship was not suspected either by Evans (1914) or by Blomquist (1940), and therefore needs careful examination. The relationship of the three American taxa to the Asiatic taxa is particularly close, and in spite of careful study, remains baffling. The three Asiatic taxa that are immediately allied are: *P. semidecurrens* Lehm. and Lindenb., *P. semidecurrens* var. *grossidens* Herzog, and *P. semidecurrens* var. *yakusimensis* Hattori. The latter taxon, described by Hattori (1948), is later placed by the same author as a synonym of the var. *grossidens* (Hattori, 1952). As we shall see, such a disposition is probably incorrect.

The interrelationships of these six taxa are so close that the student will need constant recourse to the two plates (Figs. 15, 16),

in which similar details are drawn to a uniform scale for guidance. It should be pointed out immediately that leaf-shape, and the size and number of teeth in this complex appear to vary greatly with environmental conditions; therefore these features are used in the following treatment only intraspecifically. An analysis of the six taxa suggests that they can be divided into two chief groups: (a) *P. semidecurrens* s. str., *P. semidecurrens* var. *grossidens, P. fryei* and *P. alaskana;* and (b) *P. semidecurrens* var. *yakusimensis* and *P. sharpii.* In the first of these groups we find that the cells of the leaf apices, of the leaf-middle, and of the vitta average relatively small, varying (in different races) from 12 to 15 to as high as 17-18 μ wide subapically; from 12-18 (19-20) μ wide medially, while the cells of the vitta range from 13-18 x 45-80 μ. The cells, furthermore, show a strong tendency towards development of subequally thick walls, particularly in the vitta. Even in the most robust plants, with the cells at the upper ranges indicated, the cells, especially of the vitta, are thick-walled.

In contrast, the second group includes forms with larger cells, averaging from 16.5-20, rarely to 24 μ apically and subapically; from 21-24 (rarely to 27) μ wide medially, with the cells of the vitta strongly collenchymatous, averaging 17-23 (27) μ wide x 45-70 μ long. These forms develop, in all cases, sharply defined trigones, with the intervening cell-walls thin except sometimes in the marginal and submarginal cell-rows. The cells of the vitta are noticeably less linear, and are very conspicuously provided with trigones and intermediate thickenings, so that the cell-walls become quite sinuous.

It is the present belief of the writer that each of these two groups represents a single, polymorphic species. The first group, with smaller, less collenchymatous (and more thick-walled) cells must bear the name *P. semidecurrens.* It is represented in the Sikkim-Himalaya northward to southern Japan, by the typical subspecies. From Japan to Alaska occurs a phase of this tending to have slightly larger cells and fewer and coarser teeth of the leaves; this is the subspecies *grossidens* (of which *P. alaskana* and *P. fryei* are regarded as synonyms). It occurs southward to British Columbia, where its cells attain a maximal size. The second group, characterized with slightly larger and more collenchymatous cells, must bear the name *P. sharpii,* at least for the time being. Possibly an older name will be discovered among unstudied Asiatic taxa. This species is represented in the Appalachian mountains by the typical subspecies, while a race differing in sharper, coarser and fewer teeth of the leaves supplants it in Japan (subsp. *yakusimensis* [Hattori]).

Such a conservative treatment is open to several objections. The most obvious is that each species includes plants that approach each other in the virtually identical leaves. For instance, *P. semidecurrens* subsp. *semidecurrens* has ovate-triangular leaves with numerous fine and sharp teeth; so does *P. sharpii* subsp. *sharpii.* Inversely, *P. semidecurrens* subsp. *grossidens* has oval to subrotund leaves with coarser and fewer teeth, almost exactly as in *P. sharpii* subsp. *yakusimensis.* This objection can be refuted on the basis of what we

know about the great variation, *within* each species, in leaf-shape and dentition. The Alaskan phases of *P. semidecurrens* subsp. *grossidens* show this variability to a marked degree (Fig. 16).

A second, and more serious objection, becomes apparent when long series of specimens are subjected to a careful analysis, as regards degree of development of vitta, cell size, and the form of the cell walls. Depending on the individual plant studied, we can find *average* subapical and apical cell-widths in "*P. alaskana*" and "*P. fryei*" (= *P. semidecurrens* subsp. *grossidens*) ranging from 13 to 18 μ. Similarly, *P. sharpii* subsp. *sharpii* will show variation in size of these cells from 17 to 23 μ. With study of a long series of specimens, the two species here accepted appear to merge almost imperceptibly, as regards cell size! However, in addition to the tenuous differences in cell size, we find that in the small-celled plants (= *P. semidecurrens*) there is the correlated tendency towards formation of equally thick cell-walls, particularly in the vitta, contrasted to the sharp development of collenchyma in the plants with larger cells (= *P. sharpii*).

More valid in refuting any objection to the use of cell size in this complex is an analysis *of the pattern* of variation in cell size in the different populations. In *P. semidecurrens,* for instance, the typical subspecies *semidecurrens* (Sikkim-Himalaya) has the apical cells on an average 11.5-13.5 or somewhere near 12-12.5 μ. As one moves northward to Japan, it is supplanted by the subsp. *grossidens,* the type of which has the apical cells averaging 13-15 μ in width. As one moves eastward to Alaska, we find again slight but progressive increase in cell size, with the Alaskan phase (perhaps a microrace) showing apical cells that are 14-16 μ wide (type of "*P. alaskana*") or up to 15-17 μ wide (type of "*P. fryei*"). At the southeastern edge of its range, in British Columbia, the apical cells show again a slight increase in size, ranging from 15-18 (19, rarely 20) μ. Any attempt to separate our species in this complex, on the basis of cell size is fruitless. In the more disjunctly distributed *P. sharpii* the apical cells vary from 16.5-20 (21) μ wide in the Appalachian race (subsp. *sharpii*), while the Japanese race (subsp. *yakusimensis*) has cells 18-20 μ wide, on an average. No significant difference is evident here. Confusion, on the basis of cell size, is therefore possible only between the Western American extreme of *P. semidecurrens* and *P. sharpii.* In spite of the slight overlap in cell size between these two taxa, the nature of the wall thickenings, in particular in the median cells and vitta, suggests that two different species are at hand. The marked differences in perianth-form serve to substantiate such a treatment.

The involved relationships which are here portrayed may perhaps be best summarized in the following manner:

KEY TO MEMBERS OF THE P. SEMIDECURRENS-SHARPII COMPLEX

1. Cells with finely granular oil-bodies, 2-6 per cell, small: the apical intramarginal cells 12-16 (17-18) μ wide; the median cells with ill-defined, if bulging trigones, 12-16 (17-20) μ wide x 15-22 (24) μ long; cells of vitta ± equally thick-walled, regularly rectangulate, 13-16 (18-19) μ wide x 45-80 μ long (ratio 1: 3-6); dorsal perianth keel unwinged. Himalayas to Alaska. *P. semidecurrens.* 2
   2. Leaves with marginal teeth fine, 1-3 (5) cells long x 1-2 cells wide at base, (30) 38-48 (55) per leaf; vitta well-developed; apical cells averaging 11.5-13.5 μ. Himalayas to (?) S. Japan. .... *P. semidecurrens* subsp. *semidecurrens*
   2. Leaves with marginal teeth coarser, (1) 2-4 cells wide at base, (7) 10-28 (35) per leaf; apical cells averaging 13-17 μ. Japan, to Alaska. *P. semidecurrens* subsp. *grossidens.* .... a

TABLE II.

Character	*P. semidecurrens*, Sikkim-Himalaya (Hep. Select. et Crit. No. 533)	*P. semidecurrens* (type; *fide* Herzog, 1939)	*P. semidecurrens* var. *grossidens* (type; Hep. Select. et Crit. No. 544)	*P. alaskana* (Type) = *P. semidecurrens* subsp. *grossidens* fo. *alaskana*	*P. fryei* (Type) = *P. semidecurrens* subsp. *grossidens*	"*P. semidecurrens* var. *grossidens*" (Hep. Jap. No. 180) = *P. sharpii yakusimensis*	*P. sharpii yakusimensis* (*fide Hattori*)	*P. sharpii sharpii* (Type)	*P. sharpii sharpii* (Schuster 25018)	*P. sharpii sharpii* (Schuster 25169a)
Apical cells	11.5-13.5 (15) μ	12 x 12 μ	13-15 x 13-15 μ	15-16 (-17) μ	14.5-16 (17) μ	18-24 μ	18-20 μ	16.5-20 x 18-23 μ	17-19 x 18-23 μ	17-20 μ
Median cells	14-16 (17) x 15-18 (20) μ	12 x 18 μ	12-14 x 16-22 μ	14-16 x 18-23 μ	15-17 x 18-25 μ	23-27 x 30-35 μ	24 x 27 μ	21-24 x 23-35 μ	21-25 x 25-35 μ	22-24 x 23-35 μ
Cells of vitta (and degree of development)	13-18 x 45-80 μ 1:3-6) (strong)	"pale, elongate cells" (strong)	13-15 x 45-68 μ (1:3-6) (strong)	13-16 (17) x 45-65 (72) μ (1:3-6; moderate)	14-17 (18) x 45-65 (72) μ (1:3-6; weak)	21-25 (27) x 50-70μ (1:2-3.5; weak)	20 x 50-60 μ	19-24 x 44-68 μ (1:2-4; weak)	19-24 x 45-64 μ (1:2-4; weak)	17-22 x 45-60 μ (1:2-4; weak)
No. of teeth of leaf margin	40-48 (55)	*ca.* 35-40	28-39	(20) 24-27 (35)	(7) 10-15	20-22	20-32	19-22	22-30	18-24
Teeth of leaves width x length, in cells	Fine; 1-2 x 2-3 (4)	Fine; 1-2 x 2-5	± Coarse; 2 x 5-7 to 3 x 10	Coarse but slender; 2 x 4 to 4 x 10	Coarse but short; 2-3 (4) x 2-5 (6)	± Coarse; 2 x 5 to 2-3 x 6	± Coarse; 2-3 x 4-5	Fine; 1-2 x 2-4	Fine; 1-2 x 2-4	Fine; 1-3 x 2-5
Leaf dimensions (length x width in μ)	1700 x 1550 μ	ratio *ca.* 1.2-1.4 x 1	1500-1550 x 1200-1250	1200 x 1075 μ to 1400 x 1200 μ	1050-1150 x 1300 μ to 1300 x 1500	1150 x 1300 to 1400 x 1500	2400-2600 x 1800-2000	1300 x 1050	1450-1500 x 1200-1350	1350 x 1100

a. Leaves with (20) 24-28 (35) slender, spinous apical teeth, the larger, 2-3 (4) cells wide x 3-8 (10-13) cells long; leaves ovate to oval, clearly longer than broad; vitta rather well developed; rhizoids usually rare or absent (fo. *alaskana*) to numerous (typical subsp. *grossidens*). ....Typical subsp. *grossidens* (= *P. alaskana*)

a. Leaves with (7) 10-15 shorter, broad-based, irregular teeth, 2-5 cells long; leaves ovate-triangular to subrotundate, 1.0-1.3 × as broad as long; vitta obscurely developed. Alaska. ....Subsp. *grossidens* fo. *parva* (= *P. fryei*)

1. Cells with homogeneous oil-bodies, 6-12 per cell, larger: the apical intramarginal cells (16.5) 17-20 (24) μ wide; median cells with sharply defined, bulging trigones, 21-24 (27) μ wide x 23-35 μ long; vitta of distinctly collenchymatous cells, (17) 18-23 (27) μ wide x 45-70 μ long (ratio 1:2-4); leaves with 19-30 marginal teeth; vitta rather poorly developed; perianth with dorsal keel winged. Appalachians and Japan. *P. sharpii.* 3
   3. Marginal teeth of leaves fine, 1-2 cells wide at base x 2-4 cells long usually. Appalachians. ....*P. sharpii* subsp. *sharpii*
   3. Marginal teeth of leaves rather coarse, 2-3 cells broad at base x 4-5 (6-7) cells long. Japan. ....*P. sharpii* subsp. *yakusimensis* (= *P. semidecurrens* var. *yakusimensis* Hattori, and *P. semidecurrens* var. *grossidens* Hattori, in part).

PLAGIOCHILA SEMIDECURRENS Lehm. et Lindenb. *in* L. G. et N. Spec. Hep.

Figs. 15:1-6; 16-17

Plagiochila semidecurrens Lehm. et Lindenb., *in* L. G. et N., Spec. Hep. 142, cum tab., 1840-1844; Nees, Gottsche and Lindenb., Syn. Hep. 59, 1844; Carl, Ann. Bryol. Suppl. Vol. II:98, fig. 10h, 1931; Herzog, Hedwigia 78:238, fig. 12:12, 1938; Herzog, Ann. Bryol. 12:76, 1939; Hattori, Bull. Tokyo Sci. Mus. No. 11:62, 1944; Hattori, J. Hattori Bot. Lab. No. 8:22, 1952.

Plagiochila robustissima Horikawa, J. Sci. Hiroshima Univ. Ser. B, Div. 2, I:78, Pl. 10, figs. 1-6, 1932; Horikawa, *ibid.*, II:160, 1934 (*fide* Hattori, 1952, p. 22).

Plagiochila kamuensis Tayl., J. Bot. 262, 1846.

Plagiochila shimizuana Hattori, Jour. Hattori Bot. Lab. No. 12:84, 1954 (nomen nudum).

Plagiochila semidecurrens, in its typical form, is apparently a common plant, ranging from northern India (Sikkim-Himalaya) and Nepal, to Ceylon (*fide* Stephani, 1906; p. 537), and to the montane portions of China, and (rarely, *fide* Hattori, 1952, p. 22) to Japan: Yakushima, and Formosa. The report from Japan is, according to Inoue (in litt., May 1957) incorrect. The original citation of part of the type material of the species from the Barbados is rightly considered by Herzog (1938) as the result of a careless error in labelling material. This, the typical phase, has numerous marginal teeth, all of which are fine (1, rarely 2 cells wide at base x usually 2-4 cells long). The teeth

number around 35-40 (judging from the figure of the type material in Herzog, 1938), but may go up to 48-55 (plants from the Sikkim-Himalaya here figured). In these plants the rhizoids vary, on the leafy shoots, from abundant to rather infrequent.

A closely allied plant, from Japan, described by Herzog (1938, p. 241) as *P. semidecurrens* var. *grossidens,* differs in having fewer (usually 35-40, in the examined type plants) and coarser marginal teeth. The spinous marginal teeth may range in length from 3-7 cells x 2-3 cells wide at base, but occasionally are 4-5 cells wide at base x 10-13 cells long.

Evans (1914) described two very similar plants, as *P. alaskana* and *P. fryei,* in which we find a continuation of this process of reduction in tooth-number, and in which the teeth are equally coarse, as in *P. semidecurrens* var. *grossidens.* Indeed, the variation in tooth number and coarseness of the teeth (which was one of the factors responsible for the attempt at a separation of two species from the Alaskan material), suggests that relatively little emphasis can be placed upon this as a systematic character. The Alaskan material, without much doubt, represents a mere impoverished or reduced phase of *P. semidecurrens* var. *grossidens.* The smaller size suggests this, and the smaller number of marginal teeth of the leaves appear correlated with the lesser size. In the two Alaskan plants, the reduced size is further correlated with a lesser degree of development of the basal vitta. Little or no taxonomic importance should be attached to this, however, because of the great variation in this feature in the European *P. spinulosa,* as well as in *P. sharpii* (in which weak forms may have only a slight indication of it).

In view of the very considerable polymorphism which is exhibited by *P. semidecurrens,* the writer is disposed to consider the Alaskan *P. alaskana* (and its synonym, *P. fryei*), as a mere geographical race of *P. semidecurrens,* allied to or identical with the Japanese race, *P. semidecurrens* var. (or subsp.) *grossidens.* This viewpoint (and the basis for it) is expressed in the key to this entire complex, given here on p. 264. *P. fryei,* according to this interpretation, is similar to *P. semidecurrens* var. *grossidens* fo. *parva* Hattori (Jour. Hattori Bot. Lab. 3:29, 1948). The somewhat less paucidentate *P. alaskana* seems virtually indistinguishable from some plants I have seen of typical *P. semidecurrens* subsp. *grossidens.*

Since the above study was completed I have been in correspondence with Mr. H. Inoue about the problem of the status of the two taxa described from Alaska. He also is of the opinion that *P. fryei* cannot be separated from the fo. *parva* of subspecies (or var.) *grossidens.* As regards *P. alaskana,* he believes this can be maintained as a separate variety under *P. semidecurrens,* and states that in Japan, where it also occurs, it "is a notable fact that var. *alaskana* [is] distributed at higher altitudes (mostly subalpine region) . . . than var. *grossidens.*" On a subsequent page I have given reasons for possibly maintaining *P. alaskana* as a mere forma of subsp. *grossidens.* Whatever status is assigned the plant, Inoue and I are in total agreement as to the impossibility of main-

taining it as a species distinct from *P. semidecurrens.* According to Inoue, typical *grossidens* is rather copiously provided with rhizoids along the entire leafy stem; the Alaskan plant (*P. alaskana*) nearly lacks rhizoids. The limited material I have studied suggests this difference, if it exists, is subject to considerable intergradation.

Plagiochila semidecurrens subsp. **grossidens** (Herz.) comb. n.
(Figs. 15: 4-6; 16-17)

Plagiochila semidecurrens var. *grossidens* Herzog, Hedwigia 78:241, 1938 (type issued *in* Verdoorn, Hep. Select. et Crit. No. 534, 1939).

Plagiochila alaskana Evans, Bull. Torrey Bot. Club 41:590, pl. 21, figs. 1-6, 1914; Frye and Clark, Univ. Wash. Publ. Biol. 6(3):446, 1944 (new synonymy).

Plagiochila fryei Evans, Bull. Torrey Bot. Club 41:593, pl. 21, figs. 7-9, 1914 (new synonymy; this species regarded as a synonym of *P. alaskana* by Persson, The Bryologist 49:49, 1946).

Plants in dense, compact tufts or patches, weakly *glossy,* yellowish-brown to brownish-green. Shoots 2-3 (6-8) cm long x 1.5-2 (2.4) mm wide, ascending, *rigid,* simple or with occasional branches; branches intercalary, spreading away obliquely from main stem, similar to main stem. Stems *ca.* 150-180 (210) μ thick, the brownish cortex 2-3 stratose, of thick-walled cells 15-16 (18) μ in diameter; medullary cells pale, 20-23 μ in diameter; stem *ca.* 10-12 cells high. Rhizoids usually sparse or absent on most aerial shoots, sometimes denser near their base. Leaves (in dorsal view, when *in situ*) erect-spreading, not spreading out laterally at all, the *convex dorsal fold at about a 25-45° angle with the stem,* but when plants examined laterally, the *leaves distinctly postically secund;* leaves inserted by a strongly acroscopically arched line of insertion, strongly decurrent dorsally, *short decurrent ventrally* (for less than 1/3 the merophyte length), usually slightly imbricate; leaf-shape varying from ovate to triangular-ovate and *ca.* 1-1.4 (1.65) mm long x (680-775) 1000-1250 μ wide (typical subsp. *grossidens*) to 1.05-1.4 mm long and 1.15-1.5 mm wide and suborbicular to very broadly ovate (fo. *parva*), the widest point always a $\pm$ short distance above the base; dorsal margin usually somewhat arched, *strongly revolute* to beyond the leaf-middle or to the apex, the distal portion bearing 2-8 teeth, apex rounded broadly, bearing several coarse to spinose teeth; postical margin strongly arched, dilated near base, bearing *ca.* 9-15 teeth, the leaf as a whole with a minimum of 8-12 (fo. *parva*) to usually (16) 18-25, occasionally 35 teeth; teeth varying from sharp and narrow based, 3-8 cells long and 1-3 (4) cells wide at base to somewhat coarser and broader-based and 2-5 cells wide at base; leaf-apex usually with the teeth somewhat unequal, but without indication of lobe-formation. Cells of the leaf-apex $\pm$ isodiametric, 13.5-15 (16-18) μ, near the middle 14-16 (18-19) μ x 18-25 μ, *near base forming a distinct vitta* of elongate cells averaging 13-16 (18) x 40-65 (72-75) μ; *cell-walls more or less thickened* (especially near margins), and the ill-defined trigones thus *often coalescing;* the

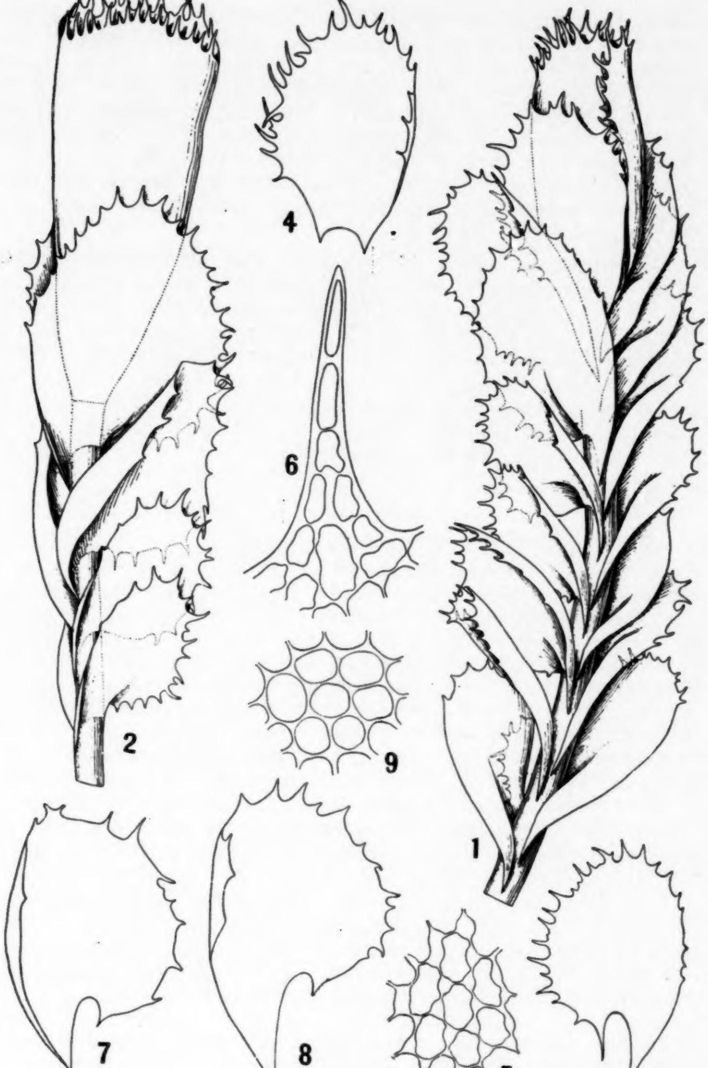

Fig. 17.—*Plagiochila semidecurrens* subsp. *grossidens* (Herz.) Schuster. 1-6. Fo. *alaskana* (Evs.) Schuster(= *P. alaskana* Evs.). 1-2. Perianth-bearing plants, antical and lateral aspects (x 23); 3. Leaf (x 23); 4. Bract (x 23); 5. Median cells (x 300); 6. Tooth of leaf-margin (x 300). 7-9. Fo. *parva* Hattori (= *P. fryei* Evs.). 7-8. Leaves (x 23); 9. Median cells (x 300). (After Evans, 1914; drawn from the types, respectively, of *P. alaskana* and *P. fryei*.)

more elongate walls occasionally with intermediate thickenings; walls of several to many rows of marginal cells usually more *strongly thick-walled and forming an ill-defined border; cells of vitta ± equally thick-walled.* Oil-bodies fewer per cell than in *P. sharpii* (2-4, less often 5-6 per subapical and median cell; 9-12 per elongate basal cell in vitta), appearing *nearly homogeneous,* but with high magnification *faintly granulose,* varying from 3 x 5 to 2.5 x 6-7 μ up to 3.3-4.5 x 9-10 μ. Underleaves small to minute, of several uniseriate capillary segments, or occasional ones several cells wide at base and divided into uniseriate cilia distally.

Male plants unknown. Female plants with inflorescences terminal, often but not invariably with 1-2 subfloral innovations; female bracts *ca.* 1.5 mm long x 1 mm wide, similar to leaves and similarly spinose-dentate as leaves (the teeth *ca.* 25, usually somewhat coarser than on vegetative leaves, occasionally 7-8 cells long x 5-6 cells wide at base). Perianth elongate, at maturity *ca.* ½ emergent beyond the bracts, the dorsal and ventral keels subequal in length, *ca.* 2-2.8 × as long as the truncation of the mouth is wide; *ca.* 2.7 mm long and 0.9-1 mm in maximum width, strongly laterally compressed, but *the keels not winged; mouth squarely truncate,* closely, sharply spinose-ciliate to ciliate-dentate.

Type.—Japan: Hondo, Kii, in monte d. Koya, *ca.* 1000 m. (*K. Sakurai, 1930*); issued *in* Verdoorn, Hep. Select. et Crit. Ser. XI, No. 534. Type of *P. alaskana* Evs. from Nichols Bay, Alaska (Frye, 1913); type of *P. fryei* Evs. from Augustine Bay, Dall I., Alaska (Frye, 1913).

Distribution.—*P. semidecurrens* subsp. *grossidens* represents the hyperoceanic, north Pacific, segment of a widespread and polymorphic species. This species, *P. semidecurrens,* has a sum-total distribution ranging from the Sikkim-Himalaya to Ceylon, northward (through the mountains of China) to Japan, and from Japan ranging to the Aleutian Islands and the humid southern coast of Alaska, southward to the Queen Charlotte Islands, British Columbia. At the south-eastern edge of its range the species grows "in shady wet areas on slope above a creek," and according to Persson (in litt.) is found "just in the waterline" along small brooks.

The subsp. *grossidens* is known from Japan (type) and from Alaska. I have seen only the type material from Japan. Other material referred to this subspecies (by Hattori, 1952) and distributed by him (Hep. Jap. No. 180) belongs to *P. sharpii* subsp. *yakusimensis.* Alaskan and British Columbian records are as follows:

ALASKA: Augustine Bay, Dall I. (*Frye* 579, 1913!); type of *P. fryei;* Nichols Bay, south end of Prince of Wales Island (*Frye* 399, 1913!; type of *P. alaskana*); Kashega, Unalaska I., Aleutian Islands (Hultén, 1932; with *Geum rossii, Luzula nivalis, Diplophyllum plicatum, Herberta hutchinsiae, Radula polyclada, Bazzania ambigua, Rhytidium,* etc.; *fide* Persson, 1946, p. 49); Ward Lake, near Ketchikan (*Anderson* 5347; *fide* Clark and Frye, 1942). BRITISH

COLUMBIA: Mt. de la Touche, Tasu Sound, Moresby Isl., Queen Charlotte Isls., 1200 ft. (*Taylor & Calder* 427!).

Differentiation.—The pluridentate, broadly ovate to suborbicular leaves eliminate confusion with all but two of our species, *P. sharpii* and *P. asplenioides.* The latter can be eliminated at once because of the much larger median leaf-cells and absence of the basal vitta, as well as by the very considerably smaller trigones, and greenish color. The separation from *P. sharpii* is more difficult. The more rounded leaf-apex, the smaller size, the tendency to produce leaves that are scarcely longer than wide usually serve to separate the two taxa. As is noted under *P. sharpii,* the variation in dimensions of the leaves of the latter is great enough to overlap those of *P. semidecurrens.* However, in all forms of *P. semidecurrens* the strongly deflexed and revolute antical leaf-margin is somewhat convexly arched (when flattened, at least). By contrast, in all phases of *P. sharpii* subsp. *sharpii* I have seen, the antical leaf margin is straight, or even slightly concave. More important systematically than all of the preceding features are the real, and apparently constant differences in oil-bodies and cell size, and in nature of the secondary thickenings of the walls. Fertile plants are at once separated by the winged dorsal perianth keel of *P. sharpii,* that of *P. semidecurrens* not being winged.

The Alaskan phases of *P. semidecurrens* differ from the Asiatic typical race *P. semidecurrens* subsp. *semidecurrens* in a relatively few, and relatively slight characters, chief among them: (a) fewer marginal teeth of the leaves; (b) a less marked basal vitta; (c) rhizoids more sparingly produced, and usually confined to the bases of the plants. In these features the Alaskan plants more closely agree with the subsp. *grossidens* from Japan, at least with the type of this and the few other specimens of it that I have seen.

At first it was believed possible to maintain the Alaskan phases as a subspecies distinct from subsp. *grossidens.* However the almost duplication of all features in the type of subsp. *grossidens* and in the type of *P. alaskana* prohibits a taxonomic differentiation. Compare here Figures 15: 4-6 and 16: 9-19. There is a slight tendency for the Alaskan plants (*P. alaskana* and *P. fryei*) to differ from subsp. *grossidens* in two respects. Firstly, the leaves tend to have somewhat fewer teeth (mostly 24-27 in the type of *P. alaskana;* but reduced to mostly 10-15 in the type of *P. fryei*) *vs.* more numerous teeth in subsp. *grossidens* (28-39 teeth per leaf). These differences are owing partly to size — the more reduced Alaskan plants thus with fewer teeth, and partly to environment — the xeromorphic, reduced type of *P. fryei* possessing highly reduced dentition. Secondly, the cells of the Alaskan plants tend to be very slightly larger. In the Alaskan plants the apical cells average 14.5-16 (17) μ, the median 14-16 (17) μ wide x 18-25 μ long; the cells of the vitta 13-17 (18) x 45-65 (72) μ. However, many leaves of the type of *P. alaskana* have the apical cells only 13.5-15 μ, the median 15 x 18-24 μ, and those of the vitta 14-15 x 40-65 μ. The latter series of measurements closely match those of the type of *P. semidecurrens* subsp. *grossidens* (see Table II) and definitely demonstrate that no constant difference in cell size exists between the Japanese and Alaskan popula-

tions. The very slight tendency, barely evident in a comparison of Figure 15: 5-6 and Figure 16: 16-18, for the Alaskan plants to have cells whose width ranges 1-2 μ higher than in the Japanese plant, is therefore evidently only sporadically expressed. The relatively robust, optimally developed plant from British Columbia (2.2-2.4 mm wide x 6-8 cm high!) shows the geographically-correlated increase in cell size to a maximal degree. The apical cells average 15-18 (19) μ; the median 19-21 x 19-24 μ; the cells of the vitta 16-18 (20) x 50-75 μ. Evidently there is progressive, if slight increase in cell size from west to east in *P. semidecurrens*. In both the Japanese type of subsp. *grossidens*, and in the Alaskan material, a very considerable variation occurs in degree of rhizoid development. On some normal, leafy stems, rhizoids are rather freely produced to near the stem apex; in other cases, rhizoids are nearly or quite absent except near the stem base. The more evident tendency for freer rhizoid production on leafy shoots in typical *P. semidecurrens* possibly serves to separate this from the subsp. *grossidens*.

Evans (1914) did not apparently perceive the immediate relationships of his Alaskan material to the Asiatic *P. semidecurrens*. He considered *P. alaskana* and *P. fryei* to be allied to *P. renitens* Nees and *P. trapezoidea* Lindenb., of India and Indonesia. These two species belong to the Sectio Renitentes Carl (1931, p. 114). Herzog (1938, p. 236) speaks of a tendency towards formation of rhizoids from the underside of leafy stems as characteristic of this group, but this is also characteristic of *P. semidecurrens*, typical, and other members of the Zonatae. Carl, *loc. cit.*, suggests that this group bears no direct relationship to the Zonatae, citing the larger, more collenchymatous cells as proof. On this basis, *P. sharpii* would go into the Renitentes, rather than into the Zonatae. However, such a distinction strikes this writer as arbitrary. Whatever position is assigned these species, they bear no direct relationship to *P. semidecurrens* and its subspecies *grossidens*, since the apical cells are fully 18-21 μ in diameter, or even somewhat larger in some Renitentes.

Variation.—Until recently, *P. fryei* and *alaskana* were considered distinct species, separated from each other by (1) the more nearly orbicular leaves of *P. fryei vs.* the more ovate leaves of *P. alaskana;* (2) the fewer and coarser teeth of the leaves of *P. fryei vs.* the more numerous and usually more slenderly spinose teeth of *P. alaskana.* Since Persson (1946) has demonstrated that specimens from the Aleutian Islands are clearly intermediate between the two types, a specific separation becomes impossible to maintain. It should be noted that in spite of the striking and obvious habitual differences between extreme plants, Evans (1914) already suggested it might not be possible to maintain *P. fryei* as a species distinct from *alaskana.*

Using a broader species concept, we find that "*P. alaskana,*" including "*P. fryei,*" shows a reasonable amount of variation in leaf-form and form of the marginal teeth. This is no greater than in such species as *P. ludoviciana* and *floridana* — and is certainly of much lesser amplitude than in *P. asplenioides.* The few available collections of this taxon prohibit a careful study of the pattern of variation at this time. Living plants have not been seen, but the writer presumes that these will be found to possess oil-bodies of the *P. sharpii* type.

On the inclusion of *P. alaskana* and *P. fryei* in *P. semidecurrens* subsp. *grossidens,* we find that this latter subspecies becomes somewhat polymorphous. The type of subsp. *grossidens* and the type of *P. alaskana* agree in the sharper, denser, more numerous, more narrowly-based and spinous marginal teeth of the leaves (see Table II). They also have oval-ovate leaves which are somewhat less prominently revolute-margined antically, *i.e.,* possess a less strongly developed cnemis. They furthermore constantly show rather narrow leaves, averaging 1.1-1.4 × as long as wide.

In contrast, the type plants of *P. fryei* have irregular, fewer (occasionally as few as 7, more often 10-15) and shorter, usually mere broad-based marginal teeth. They also have subrotund leaves that average as broad, or broader, than long (although the exact proportions cannot readily be determined, since the cnemis is so strongly developed that the revolute antical margin cannot be flattened out under pressure). The increased width in the leaves of *P. fryei* is largely owing to the dilation above the postical base, resulting in a more highly arcuate postical leaf margin. No other differences between *P. fryei* and the type of *P. alaskana* (and *P. semidecurrens* var. *grossidens* type) are evident; the cells are identical in size and closely match those of the type of *P. alaskana* in the development of trigones. The writer would conclude that *P. fryei* represents merely an impoverished, xeromorphic extreme of *P. alaskana,* and therefore of *P. semidecurrens* subsp. *grossidens.* The rather marked morphological differences perhaps warrant its recognition as a distinct forma; it should, if such recognition is deemed desirable, bear the name *P. semidecurrens* var. *grossidens* fo. *parva* Hattori (Jour. Hattori Bot. Lab. No. 3:29, 1948). The following synonymy is therefore necessary:

Plagiochila semidecurrens subsp. *grossidens* (Herz.) Schuster

fo. *alaskana* (Evans) Schuster

Plagiochila alaskana Evans, Bull. Torrey Bot. Club 41:590, 1914 (new synonymy).

Plagiochila shimizuana Hattori, Jour. Hattori Bot. Lab. No. 12:84, 1954 (nomen nudum).

fo. *parva* Hattori

Plagiochila fryei Evans, Bull. Torrey Bot. Club 41:593, 1914 (new synonymy).

Plagiochila semidecurrens fo. *parva* Hattori, Jour. Hattori Bot. Lab. No. 3:29, 1948.

PLAGIOCHILA SHARPII Blomquist

Plagiochila sharpii Blomquist, The Bryologist 43:90, figs. 1-12, 1940.

Plagiochila semidecurrens var. *yakusimensis* Hattori, J. Hattori Bot. Lab. 3:29, fig. 37, 1948.

Plagiochila semidecurrens var. *grossidens* Hattori, Hep. Jap. (Exsiccatae), No. 180, 1951 (not of Herzog, 1939).

Plagiochila sharpii is here defined as a polymorphic taxon, closely allied to *P. semidecurrens,* of the Sikkim-Himalaya, Japan, and oceanic Alaska. It appears to differ from *P. semidecurrens* in several important respects: (a) the cells of the leaves are markedly larger (See Table II); (b) the basal vitta of the leaves is much less prominently

developed; (c) the leaf cells are everywhere more sharply and prominently collenchymatous.

The species is considered to include two closely allied plants, one endemic to the Southern Appalachians (subspecies *sharpii*), the other to the island of Yakushima, Japan (subsp. *yakusimensis*).

Plagiochila sharpii subsp. **yakusimensis** (Hattori) comb. n.
Fig. 15: 10-12

P. semidecurrens var. *yakusimensis* Hattori, J. Hattori Bot. Lab. 3:29, figs. 37, 1948; Hattori, J. Hattori Bot. Lab. 8:22, 1952 (as a synonym of *P. semidecurrens* var. *grossidens*).

P. semidecurrens var. *grossidens* Hattori, Hep. Jap. (Exsiccatae), No. 180, 1951; Hattori, J. Hattori Bot. Lab. 8:22, 1952 (not of Herzog, 1939).

Plants similar in aspect to subsp. *sharpii,* somewhat larger at times (leaves to 1800-2000 μ wide x 2400-2600 μ long). Leaves broadly ovate-triangular to ovate-orbicular, narrowly rounded at apex. Marginal teeth of leaves rather coarse, 2-3 (4) cells broad at base x 4-5 (6-7) cells long, rather few (20-32) per leaf. Apical cells 18-20 μ, thick-walled; median cells *ca.* 24 x 27 μ, with coarse, nodular to confluent trigones; cells of vitta 20 x 50-60 μ, with sinuous walls due to distinct trigones and intermediate thickenings; oil-bodies nearly smooth, of exceedingly delicate granulae, almost homogeneous, 5-8 per cell, in vitta *ca.* 10, from 3 x 4-9 to 4 x 4-6 μ, in median cells, those in the vitta to 4 x 9-12 μ (*fide* Hattori, 1951).

Type.—Japan (No. 7474, in herb. Hattori Botanical Laboratory).

Occurrence.—Dr. Hattori informs me (in litt.) the type material was "growing in a tuft on humus covered granitic rocks in dense, primeval evergreen forest."

Distribution.—According to Hattori (1952, p. 22) endemic in the montane area of the Island of Yakushima (S. Japan), *ca.* 30° N. Lat., 130° E. Long.

An interesting parallelism exists between the distribution of *P. sharpii yakusimensis* and that of *P. s. sharpii* in the Southern Appalachians, which are both montane, and the analogously distributed *P. yokogurensis,* with typical, Japanese subsp. *yokogurensis:* "Not uncommon, preferrably at low elevations" (Hattori, 1952, p. 23), while the subsp. *fragilifolia* is also found at low elevations (0-2000 feet) on the eastern slopes of the Appalachian system, into the Coastal Plain. There is not only a parallelism in general geographical distribution, but, within the two general areas the related subspecies have a similar restriction altitudinally.

P. sharpii subsp. *yakusimensis* differs from the typical subspecies in several relatively slight features, among them: (a) coarser marginal teeth of the leaves; (b) oil-bodies averaging slightly fewer per cell, particularly in the cells of the vitta, and with a distinct (if faint) indication of granulae, rather than quite homogeneous; (c) an evidently

somewhat larger maximal size. To what degree these differences, derived from study of only limited Japanese material, will maintain themselves is questionable. However, no plant has been seen in the Southern Appalachians with the marginal teeth of the leaves as coarse as those of the Japanese material. The relationship between *P. s. sharpii* and the subsp. *yakusimensis* is thus quite analogous to that between *P. semidecurrens* subsp. *semidecurrens,* and *P. semidecurrens* subsp. *grossidens,* the latter being the coarser-dentate derivative of the finely dentate typical *P. semidecurrens.*

The material labelled "*P. semidecurrens* var. *grossidens*" and distributed by Hattori (Hep. Jap. No. 180) represents an xeromorphic form, with very broad, suborbicular leaves (averaging slightly to distinctly wider than long, exactly as in extreme forms of *P. sharpii* subsp. *sharpii*). These plants agree closely with *P. sharpii* in the size of apical, median, and basal cells. They further possess a very weakly developed vitta, and have a reduced number (20-22) of marginal teeth, as is commonly the case in *P. sharpii.* These plants differ from *P. sharpii* essentially in two points: the marginal teeth of the leaves are somewhat coarser, and the antical margin of the leaves is more strongly revolute. The more strongly revolute antical leaf margin results in a leaf that cannot be flattened out under pressure. By contrast, in *P. sharpii* subsp. *sharpii* the leaves are usually readily flattened out under pressure, since the cnemis is less sharply marked. There appears to be a clear parallel here between *P. sharpii yakusimensis* and *P. s. sharpii,* on one hand, and *P. semidecurrens grossidens* (= *P. alaskana*), and the xeromorphic fo. *parva* of the latter. In both instances, the broader-leaved, more ampliate, xeromorphic phase possesses a more sharply revolute antical leaf-margin. It is probable that this difference is environmental in origin — or at least accentuated by environmental causes. The type of "var. *yakusimensis*" of Hattori, which its author later reduced to a synonym of *P. semidecurrens* var. *grossidens* I have not seen. The pertinent measurements of it (taken from Hattori) clearly show a close correspondence with the material distributed by him as "var. *grossidens*" (nec Herzog). However, the var. *yakusimensis* is stated to be a larger plant, with leaves to 2.6 mm long.

From the material studied by the author, *P. semidecurrens* var. *grossidens* of Hattori (not of Herzog!) = var. *yakusimensis* Hattori, appears specifically inseparable from *P. sharpii.* The discovery of broadly ovate-triangular leaved, deep brown, xeric phases of *P. sharpii* (Fig. 18: 2-4) demonstrated that there is no essential difference in leaf-shape between these taxa. As shown (Table II), the cell-sizes correspond closely. If the illustrations given by Hattori for the first two taxa are compared with those given here for *P. sharpii,* and those given by Blomquist (1940), it is clear that there is no difference in the mode of thickenings of the cells that can be used to affect a separation of these plants.

Admitting the similarity of the Japanese and Appalachian plants, the problem arises as to the correct nomenclature of these plants. The writer is disposed to regard the above material, figured (and distributed) by Hattori, as specifically distinct from *P. semidecurrens* and *P. semidecurrens* var. *grossidens* Herzog. The differences in cell size, and in number of marginal teeth of the leaves, are impressive. On the other hand, this material, *i.e.,* "*P. semidecurrens* var. *grossidens*" as distributed by Hattori (Hep. Jap. No. 180), is close in many respects to *Plagiochila fryei* Evs., from the oceanic coastal portion of Alaska. The two taxa share the same leaf-shape, with (in many cases) leaves that are strongly ampliate and fully as wide as long; they have somewhat coarser and fewer

marginal teeth than in typical plants of *P. sharpii*. However, the xeromorphic plants of *P. sharpii* (Fig. 18: 2-4) may have only 17-22 marginal teeth, and very similarly shaped leaves.[2]

However, *P. fryei* has somewhat smaller leaf-cells than the Japanese material alluded to, and than *P. sharpii*. It, and the very similar *P. alaskana*, closely approach *P. semidecurrens* in cell size. The writer would therefore retain the name *P. sharpii* for the larger-celled plants, with poorly developed vitta, and with rhizoids sparse or absent, except at base of stems. The Appalachian phase of the species would become the typical subspecies *sharpii;* the plants from Japan should probably bear the name *P. sharpii* subsp. *yakusimensis* (Hattori) comb. n., since they appear to be racially distinct from the Appalachian.

PLAGIOCHILA SHARPII subsp. SHARPII Blomquist
Figs. 15:7-9; 18-20

Plagiochila sharpii Blomquist, The Bryologist 43:90, Figs, 1-12, 1940.

Plants in large, often dense mats, with the appearance of a *shiny,* olive-green or brownish *P. asplenioides,* forming tufts often (1) 2-3 cm thick, with the plants closely matted; individual shoots a dull green or olive-green to brownish green, *shiny when dry,* (1.2-1.5) 2.3-2.8 mm *wide* with the leaves, *ca.* 2-3 cm long, ascending to recumbent. Stems *ca.* 240-285 μ in diameter, the aerial *stems simple or nearly,* diffusely, usually monopodially (rarely subdichotomously) branched; cortical cells in 2-3 strata, thick-walled, oblong to rectangular, the medullary relatively thin-walled, sharply separated from the cortical, larger in diameter and much more elongated; stems *ca.* 12-15 cells high. *Rhizoids virtually absent, except on stoloniferous stems and at bases of aerial stems.* Leaves of main shoots $\pm$ spreading laterally, varying from 45-70° in angle to stem-apex (but usually 55-70° on older shoots), erect to erect-appressed when dry, when moist *strongly postically secund,* approximate to moderately imbricate, asymmetrically triangular-ovate, to ovate-orbicular, with *antical margin nearly straight to slightly concave,* the postical margin strongly dilated basally and from the dilated base on weakly arched to nearly straight; leaves *ca.* (0.95-1.2) 1.5-1.6 (1.75) mm long x (0.85-0.95) 1.3 mm wide at widest, subbasal point, (1.0) 1.2-1.4 *as long as wide,* inserted by a very long line of insertion, the dorsal base long-decurrent, the *postical-base short-decurrent;* antical margin strongly decurved and *often revolute from near base to near apex,* with median base depressed (to about midway to apex), the cnemis therefore strongly developed, forming

[2] Subsequent to the completion of this section, high-altitude forms of *P. s. sharpii* have been seen (6050-6500 feet, in North Carolina) which even more closely approach *P. s. yakusimensis* in the rather broad leaves, with the whole antical margin broadly and strongly involute, and with the apex and postical margins of the leaves bearing often only 10-18 teeth, some of which are coarser than is normally the case. The occurrence of such plants in North America strongly reinforces the previously expressed opinion that *yakusimensis* is specifically identical with *sharpii.*

a strongly convex dorsal fold; leaf-margins with (17-18) *20-26* (32) *teeth on mature leaves,* of which 1-4 occur near apex of antical margin, and *ca.* 16-20 (24) along the entire postical margin, extending down to the base of the decurrent postical strip, the rest apical; apical teeth usually not more pronounced than others, but sometimes more coarse,

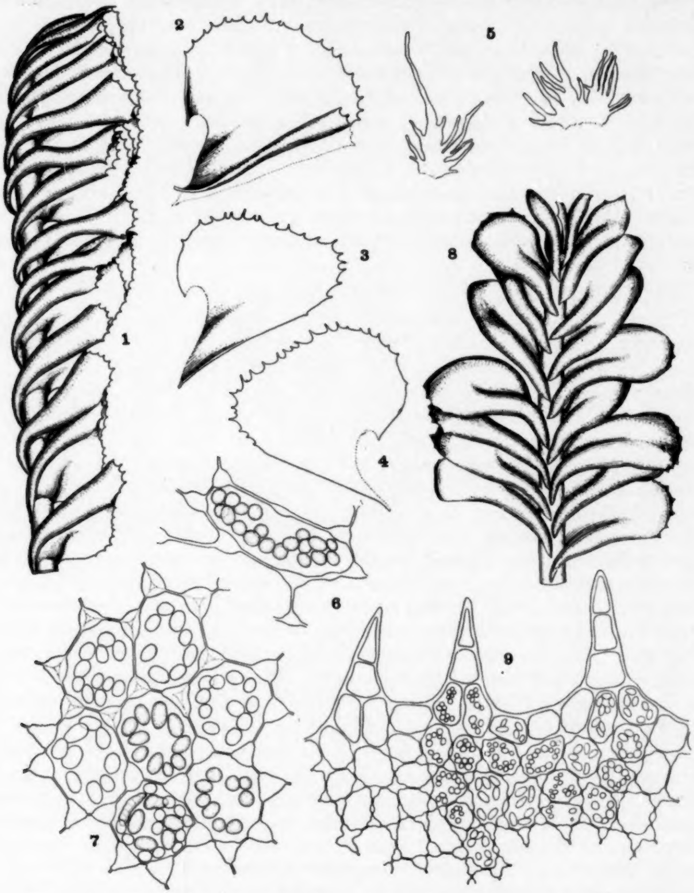

Fig. 18.—*Plagiochila sharpii* subsp. *sharpii* Blomquist. 1. Lateral aspect of shoot (x 17); 2-4. Leaves (x 19); 5. Two underleaves (x 67); 6. Cells from vitta, showing oil-bodies (x 460); 7. Median cells, mod. *mesoderma* (x 500); 8. Shoot-apex (x 17); 9. Cells of postical margin (x 250). (Figs. 1-4, 8, Whitewater Gorge, N. C., *Schuster* 25003, a deep-brown mod. *colorata-pachyderma;* 6-7, 9, same locality, *Schuster* 25007, a more greenish mod. *viridis-mesoderma.*)

the leaf thus somewhat bidentate at apex; teeth moderate in size, 1-5 (mostly 2-3) cells long, mostly 2 cells wide (but apical teeth when larger occasionally to 4-5 cells wide); *apex narrowly rounded,* rarely narrowly truncate, with usually 2-3 teeth. Branch leaves similar to main leaves, but often with fewer teeth. Cells with the marginal 2-3 rows with trigones often indistinct, *usually ± strongly thick-walled;* interior cells with *strong, bulging trigones;* interior cells from 17-18 (21) μ or 18 x 25 μ apically to 21-24 x 25-30 (35) μ medially; cells on posterior margin, near leaf-middle, 16-22 x 21-24 μ; basal median cells of vitta *ca.* (16) 18-22 x 42-52 (60-72) μ; cuticle smooth; *oil-bodies smooth, homogeneous, small,* 4-5 μ and spherical to 4 x 5-6 > 4.5 x 8-9 μ, *relatively numerous* (6-10, occasionally 12 per median cell; in vitta 15-20 (24) per cell). *Underleaves small to minute,* often mere stalked slime papillae, sometimes of a single row of cells, ending in a slime papilla, at other times larger, ending in 3-9 (15) rows of uniseriate cilia each terminated by a slime papilla. *Asexual reproduction absent.*

Male inflorescences yellowish (standing in obvious contrast to rest of plant), narrow and compactly spicate, terminal but eventually apparently always intercalary, rarely branched, often with 1-2 subfloral innovations; male bracts smaller than leaves, usually of 8-10 pairs of closely imbricate bracts whose suberect, ventricose bases are strongly imbricate; basal one-half to two-thirds of perigonal bracts erect, the distal lamina erect-spreading; margins usually with fewer teeth than vegetative leaves; antheridia usually 2-4 per bract. Gynoecia (very rare!) terminal on leading leafy axes, *always with one or two innovations;* if with single innovation, the perianth becoming pseudolateral and the innovations becoming vigorous, usually again fertile; if with paired innovations, the innovations usually remaining short and sterile (rarely two innovations issue from the axil of the same bract; both then may be elongate and fertile). Innovations originating variously: sometimes in axil of the bract or bracts, sometimes originating immediately behind the bract; if with two innovations usually one axillary in bract, the other originating below the opposing bract, but sometimes both innovations axillary in the bracts. Bracts very similar in shape to the leaves, asymmetrically ovate-triangular, *ca.* 1500-1600 μ long x 1050-1250 μ broad (at the widest portion, *ca.* one-fourth the distance from base to apex), longly decurrent antically, the nearly straight antical margin broadly and conspicuously reflexed-convolute, edentate in the basal 0.4-0.5, distally with 3-7 small, sharp suberect teeth; apex narrowly subtruncate, with 2 coarse and often a third median smaller tooth; postical margin strongly ampliate at and immediately above the base, the distal 0.65-0.75 nearly straight, the postical margin with 25-30 sharp, somewhat separate, somewhat irregular spinose teeth varying from 2-5 (7) cells long x (1) 2-3 cells wide at base, the teeth similar to those of the leaves, but often with the *basal 2-4 teeth hooked and reflexed.* Perianth in antical aspect narrowly ovoid with compressed mouth, rather strongly inflated basally and less so above, but

the region around the *rounded mouth* strongly compressed, the perianth thus mussel-shaped and bilabiate; in lateral profile perianth *obovate-obdeltoid with a broadly rounded mouth,* each of whose lips bears 16-20 irregular-sized, acuminate, sharp teeth, which vary from 2-3 cells long x 2 cells wide at base up to 10 cells long x 3-4 (5) cells wide at base; antical and postical keels commonly subequal in length (but the postical often shorter, sometimes obsolete), the *antical usually with a broad wing* (*to 10-12 cells wide*) bearing 0-2 teeth, often ending 0.5-0.6 from apex of keel, sometimes complete; postical keel with a narrower, often edentate wing that is frequently complete to apex of keel. (Diagnosis of perianth based on plants with unfertilized perianths; these in part atypically developed and incised to the base postically).

Type.—Whitewater River Gorge, Jackson Co., North Carolina, *Anderson* 6636 (Duke!).

Distribution.—Endemic to the Southern Appalachians. Previously reported (Blomquist 1940, Frye and Clark, 1945) from North Carolina and Tennessee, but also found by the writer to extend into the escarpment region, where the Appalachians drop off into the Piedmont, in northern South Carolina, there at its lowest elevation (*ca.* 1800 ft.); at its highest elevation almost extending into the Spruce Fir forests (4000-4500 ft.), rarely into it (6050-6500 ft.).

TENNESSEE: Sevier Co.: foot of Ramsey Prong, Greenbrier (*Sharp* 3886!); Pinnacle Trail, Greenbrier, 3000 ft. (*Sharp* 34596!); Greenbrier, 2700 ft. (*Sharp* 3882!) (cotype); near Rainbow Falls, Mt. Le Conte, 4500 ft. (*Sharp* 34479!); W. branch of Little Pigeon R., *ca.* 4000 ft., near Chimneys Parking Area, Smoky Mts. Ntl. Park (*Schuster* 36541); Roaring Fork, Mt. Le Conte, 4000 ft. (*Sharp* 34518!); above the Orchard, Mt. Le Conte (*Sharp* 3569). NORTH CAROLINA: Below High Falls, Whitewater R., Jackson Co. (*Schuster* 25031, 2517a, 25005, 34735, 25018, 25008a; 25052, with *P. virginica caroliniana; Anderson* 6636); Whitewater R. gorge, Transylvania Co. (*Schuster* 25051, 25056, 25003, 25007, 25003a; 25004, with *P. caduciloba;* 25004a); Chattooga Cliffs, near Highlands, Macon Co. (*Anderson* 8634!); Wolf Creek near junction with E. fork of Tuckaseegee R. (*Anderson* 10225!); Chestnut Bald, Balsam Mts., 6050 ft., SE. of Sunburst, in spruce-fir zone (*Anderson* 11176, 11180, 11178, 11170, p. p. with *P. caduciloba;* 11177, p. p. with *Metzgeria conjugata*); Devil's Courthouse, 5500 ft., on bark of *Betula lutea,* Spruce-fir zone, Transylvania Co. (*Anderson* 1146, p. p. with *Harpalejeunea ovata*); Thompson R. gorge, 4 mi. SE. of Bohaynee, Transylvania Co., 2500 ft. (*Anderson* 11098); Devil's Courthouse, *ca.* 5500 ft., Transylvania Co., S. of Blue Ridge Parkway (*Schuster* 39481; on bark of *Abies fraseri!*); Chattooga R., at the Narrows, and just above the bridge across on Forest Route 31, 4.5 mi. SE. of Highlands, Macon Co., 2500 ft. (*Schuster and Bryan* 39437, *c. per.!,* 39437a, 39810 [39810, p.p. with *P. caduciloba, P. asplenioides, Radula obconica, Lejeunea lamacerina gemminata* and *Lophocolea muricata*]); Chattooga R., E. bank just above Ellicott Rock, above Ga.-S.C. state lines, Jackson Co., 2100 ft. (*Schuster and Bryan* 39856); branch from Fork Ridge, just above jct. with W. Fork Pigeon R., 4500-4600 ft., above jct.

of Flat Laurel Cr., S. of Sunburst, Haywood Co. (*Schuster* 38741). SOUTH CAROLINA: Gorge of Whitewater R., *ca.* 4-5 mi. NW. of Jocassee, Oconee Co. (*Schuster* 25169a); E. bank of Chattooga R., 0.1-0.8 mi. S. of Ellicott Rock and N.C. state line, N.W. corner Oconee Co., 2000-2100 ft. (*Schuster and Bryan* 39902, 39903). GEORGIA: W. bank of Chattooga R., 0.1-0.8 mi. S. of Ellicott Rock, NE. corner of Rabun Co., 2000-2100 ft. (*Schuster and Bryan* 39832, 39839 (*c. per.*), 39869a, 39869b, 39834a, 39871b, 39900; the species barely penetrating into Georgia; associated with *P. caduciloba, P. asplenioides, Tritomaria exsecta, Radula obconica* and *Lophocolea muricata*); about 0.2 mi. below High Falls of Big Creek, *ca.* 5 mi. S. of Highlands, N.C. in northern Rabun Co., 1900-2000 ft. (*Schuster* 40041, 40051, *c. per. p.p.*, with *Plagiochila caduciloba*).

Occurrence.—Nearly restricted to the deep, dense undifferentiated luxurious forests of the Southern Appalachians, where it is found at elevations from *ca.* 1800 ft. to at least 4000 ft. Apparently it is found exclusively on moist siliceous rocks, often as a pioneer (then frequently with *Plagiochila caduciloba* and *sullivantii, Harpalejeunea ovata,* less often *Leucolejeunea clypeata*), and then in diffuse mats, with the suberect aerial shoots at some distance from each other. Often persisting until the rocks are covered with thin soil-layers, then forming thick, dense mats, often in admixture with *Plagiochila asplenioides* (which stands out by the purer green of the plants). Under the wettest conditions the species occasionally occurs with *Scapania nemorosa, Marsupella sphacelata,* etc. Under the most shaded conditions, the fern *Trichomanis petersii* is frequently consociated.

The species also occurs, apparently very locally and only in the area of the Balsam Mts. of North Carolina, in the Fraser Fir-Red Spruce forest, at from 6000-6500 ft. It is found here either on shaded boulders, or moist shaded ledges, associated with *Plagiochila caduciloba, Metzgeria conjugata,* and *Marsupella paroica.* More infrequently it occurs on the bark of *Betula lutea,* as a small phase with the vitta obsolete, associated with *Harpalejeunea ovata.* Similar, small phases have also been found at lower elevations, again on *Betula* (*B. lenta*), associated with *Plagiochila caduciloba, Lejeunea ruthii, L. laetevirens, Leucolejeunea clypeata, Harpalejeunea ovata, Frullania asagrayana, Radula obconica, Metzgeria furcata* and *M. crassipilis.* Such corticolous occurrences are rare and depend obviously on a saxicolous "reservoir population."

Variation.—*P. s. sharpii* appears to be a moderately variable taxon, judging from the available material. The type specimen has the leaves, in antical aspect, widely spreading from the stem and has relatively small cells (minimal figures for the various areas quoted in the description). The figures cited by Blomquist (1940) are smaller than those given here, since they are based on *lumen* and not *cell diameters.* However, the material from Tennessee (*Sharp* 34518, 3882) has the leaves often spreading at an angle of only 45-50° from the stem-apex (Fig. 20:1-3), giving the plant a considerably different appearance. Most material seen, including that collected by the author (gorge of Whitewater R., Transylvania Co., North Carolina, Aug. 18, 1952,

Schuster 25003) possesses slightly larger leaf-cells (maximal figures quoted in the description above). This material also has the marginal cells with the walls between the trigones little or not thickened, thus with the trigones of the marginal cells evident and as knot-like as those of the median cells (Fig. 18:9). Study of a series of specimens bridges these slight differences completely.

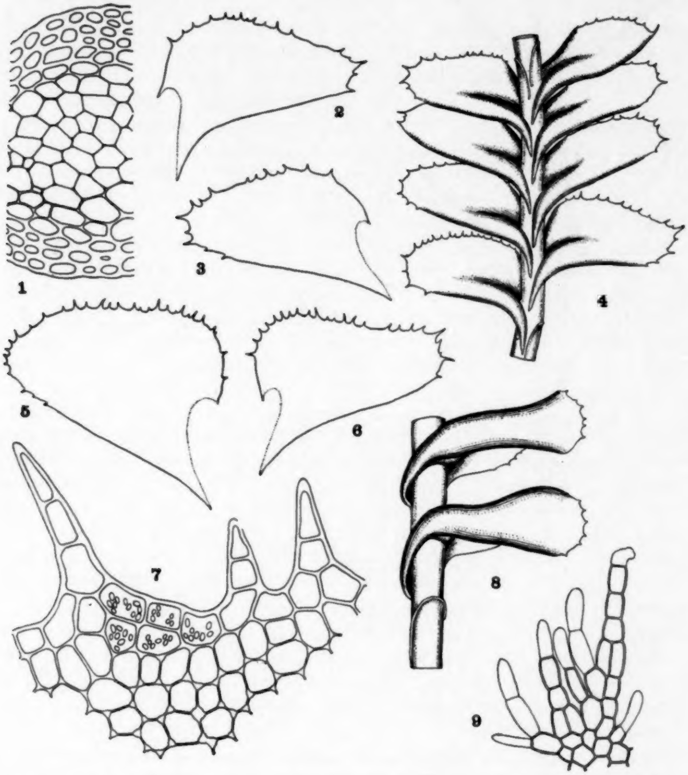

Fig. 19.—*Plagiochila sharpii* subsp. *sharpii* Blomquist. 1. Stem cross-section, from large shoot (x 165); 2-3. Leaves (x 17.3 and 19.7); 4. Part of shoot of greenish mod. *angustifolia* (x 15); 5. Leaf of mod. *viridis-mesoderma* (x 15); 6. Leaf of mod. *angustifolia* (x 16); 7. Cells of mod. *viridis* (x *ca.* 275); 8. Part of shoot, xeric brown phase in fig. 18:1-4, 8 (x 20); 9. Half of large underleaf (x 175). (All from plants from Whitewater R., N. C.; 1, from *Schuster* 25018; 2-4 6, from *Schuster* 25031, mod. *angustifolia;* 5, 7, from *Schuster* 25007, mod. *viridis-mesoderma;* 8-9, from *Schuster* 25003, mod. *colorata-pachyderma.*)

To what degree differences in cell-size and degree of development of the border are genetically controlled, and to what degree environmentally controlled, appears quite uncertain. The large-celled ma-

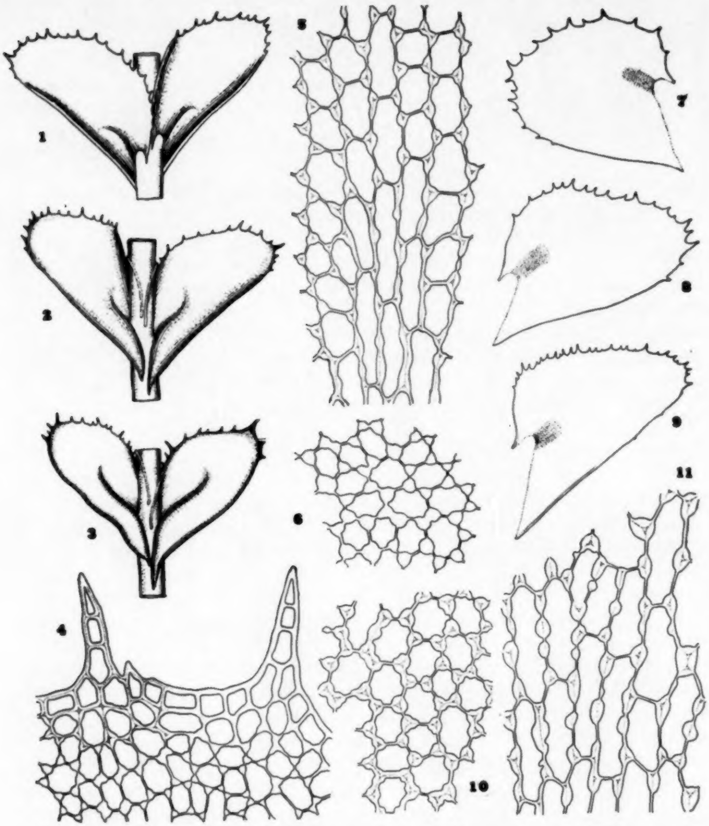

Fig. 20.—*Plagiochila sharpii* subsp. *sharpii* Blomquist. 1-3. Shoot-sectors showing the oblique to suberect leaf-orientation, in 1, postical, in 2-3, antical aspects (x 20); 4. Marginal leaf-cells, showing maximal development of border (x 205); 5. Cells of leaf-base, showing extreme with slight development of vitta but with the cells unusually narrow, somewhat abnormal (x 205); 6. Subapical cells (x 205); 7-8. Broad leaves (x *ca.* 20); 9. Leaf of typical form (x *ca.* 20); 10. Subapical cells (x 240); 11. Normally developed cells of vitta basalis (x 240). (Figs. 1-4 from *Sharp* 34518, Mt. Le Conte, Tenn.; 5-8, from *Sharp* 3569, Mt. Le Conte, as *"P. ludoviciana"*; 9-11, from *Schuster* 25018, Whitewater Gorge, N. C.; figs. 4-6 drawn to same scale as corresponding figures in Fig. 15:1-12.)

terial (*Schuster* 25003) also represents a very dense-leaved modification (with the leaves much denser than in the type), in which the leaves are not laterally spreading, but are suberect as viewed dorsally (at an angle of *ca.* 45° with the stem), much as in *P. semidecurrens.* It would appear, therefore, that xeromorphic forms (and *Schuster* 25003 represents a xeromorphic extreme, from thinly soil-covered, relatively exposed rocks) with their suberect leaves that do not spread at all laterally, differ considerably from the mesic extreme of shaded rocks, with distant to subimbricate, more laterally spreading leaves. *P. s. sharpii,* therefore, undergoes a relatively broad range of modification concurrent with its relatively wide toleration of differences in light intensity and saturation deficit.

The characteristic orientation of the leaves is scarcely evident when we examine the plant dorsally (although even then we can usually see that the leaves are postically deflexed). In lateral view the xeromorphic forms (such as *Schuster* 25003a) show the characteristic leaf-form very readily (Fig. 18:1). We find, then, that though appearing to spread at an angle of 45° from the stem (as examined dorsally), these shoots really bear leaves that are very strongly postically deflexed or secund, even when wet. This is true, it must be admitted, largely for the xeromorphic forms, which are brownish pigmented and relatively small (shoot width 1.2-1.5 mm). Such plants differ very strongly from the relatively lax-leaved type figured by Blomquist, from which one gets the impression of a plant with laterally spreading and not deflexed leaves. In the dorsally suberect appearing leaves, but laterally strongly postically deflexed leaves, the more xeromorphic extremes of *P. sharpii* are so closely similar to "*P. alaskana*" (=*P. semidecurrens grossidens*) that separation is exceedingly difficult. This is true not only for leaf-orientation and size, but also for leaf-shape. Since Blomquist has stressed this as one of the chief differences of his species, from "*P. alaskana,*" the following detailed comparison of the leaf-shape of the two species is pertinent.

Perhaps the most significant amount of variation—and the most distressing from the point of view of recognition of the species—is found in the leaf-shape. The more or less lax-leaved forms (such as the type material figured by Blomquist), with relatively elongate leaves (1.6 mm long x 1.3 mm wide; in some of my material as much as 1.95 mm long x 1.6 mm wide), *i.e.,* with the leaves *ca.* 1.2-1.4 × as long as wide, have the leaves widely spreading (as in Blomquist, 1940, figs. 1-2); such material represents the mod. *laxifolia-angustifolia-patulifolia,* with relatively long internodes. This represents the modification of deep shade and low saturation deficit (Fig. 19: 2-6).

However, under the drier conditions noted above we find that not only does the leaf become denser (internodes shorter), and the leaf less laterally spreading, but the leaf becomes progressively shorter. For instance, the xeric form (*Schuster* 25003, Whitewater Gorge, Fig. 18: 1-4), has notably shortened leaves, whose dimensions vary from 975 μ wide x 1080 μ long to 1250 μ wide x 1320 μ long, to an extreme of

1125 μ wide x 1050 μ long: *i.e.,* the strongly ampliate leaves become subequal in length and width, or even slightly broader than long, and become broad-ovate to suborbicular. Such plants have the leaves not only shaped somewhat like those of "*P. fryei,*" but have them suberect as in the latter. In extreme cases (corticolous populations) a similar reduction in dentition takes place.

The amplitude of variation in leaf-form and orientation of the leaves in *P. s. sharpii* is therefore great enough to suggest that, were it not for the larger cells, it might be included within *P. semidecurrens* as a subspecies, rather than treated as a discrete species. The pronounced differences in the perianths suggest, however, that two fully discrete species are at hand. It should be pointed out that the dimensions of the leaves in the xeromorphic forms of *P. sharpii* (considerably less than 1.4 x 1.4 mm) agree closely with those of the xeromorphic form of "*P. alaskana*" (= *P. fryei*), in which they are reported as 1.4 mm long x 1.2-1.4 mm wide.

Perhaps the most extraordinary extreme of *P. s. sharpii* which has been found is material of a mod. *parvifolia-subdentata,* whose leaves average only about 550 μ wide x 750-800 μ long. These plants, growing 3-4 ft. high on the bark of *Betula* (*Schuster* 34735, Whitewater Gorge, N.C.) occurred with a small phase of *P. caduciloba,* with *Lejeunea ruthii* and *laetevirens, Leucolejeunea clypeata, Harpalejeunea ovata, Frullania asagrayana, Radula obconica,* and *Metzgeria furcata* and *crassipilis.* The leaves bore only 5-7 obscure and often merely acute teeth; the cells were strongly collenchymatous, averaging 17-22 μ subapically, to 23 μ medially; the vitta was virtually absent, only a very few basal cells being distinctly elongated. In the few-dentate leaves and essential suppression of the vitta these plants are totally deviant. The presence of glistening homogeneous oil-bodies and coarse trigones, and the ovate leaf-shape clearly place them in *P. sharpii.* However, they very closely approach some of the small corticolous phases of the European *P. spinulosa,* from which they differ perhaps most essentially in the smaller leaf-cells. The plants are of further interest in that they squarely pose the question of the dissemination of *P. s. sharpii,* the normal phases of which have never been seen with spores or asexual propagula. On a few of these corticolous plants isolated leaves were broken free — although clearly not caducous in the strict sense of the term. Also, on one of the persistent leaves, on the abaxial face near the leaf-base, several small, few-celled cell-masses were found, forming an approach to discoid "gemmae." It is possible that these cell-masses or plates, evidently very rarely developed, represent a type of regeneration or primitive "propagula." In any case, *P. s. sharpii* never reproduces by any of the "normal" asexual modes that characterize our other species.

Perianths in this species are very rarely produced; I have seen them only in material from the Chattooga R. (*Schuster and Bryan* 39437) and in plants from below the High Falls of Big Creek, Georgia (*Schuster* 40051); by contrast, androecial plants are very widely distributed and readily found. The perianth form in this taxon is very variable, but several general distinctions from that of *P. semidecurrens* appear to be uniformly present. Firstly, the perianths are, at least if sporophytes are not developed, much broader and obovate to narrowly obdeltoid or broadly obcuneate in lateral profile, with the mouth broadly rounded. Secondly, the mouth bears strongly variable

teeth, which vary very greatly in length and size. Thirdly, the perianth-keels are shorter, and are winged. The antical keel is always well-developed and varies from 1-1.5 × as long as the width of the perianth at the mouth; it is always sharply winged in the basal 0.4-0.6 of the keel, with the wing rarely extending to the sinus between the perianth-lips; the wing is up to 10-12 cells wide and may be edentate, ending gradually above, but is most often 1-2-dentate. The postical keel wing is much more variable in the degree to which it is developed; it may, exceptionally, be lacking, but is usually present as a lamella 2-3 cells wide, that is most often edentate and frequently runs up the entire keel.

The bracts are also different in shape than in *P. semidecurrens,* being widest just above the base, with the postical base strongly dilated, the fundamental shape being narrowly ovate-triangular and strongly asymmetric; in *P. semidecurrens grossidens,* at least, the bracts are obovate to elliptical in shape, with a nearly symmetric form. Although Evans states that the Alaskan plants of *P. semidecurrens grossidens* frequently bear 1-2 subfloral innovations, he illustrates two plants that lack innovations. I have not seen a single plant of *P. sharpii,* among hundreds examined, in which innovations were lacking. Although the innovations are generally as described in the diagnosis, occasionally *P. sharpii* shows freer branching associated with perianth production than has been indicated. For example, one luxuriant aerial shoot showed a primary gynoecium with two strong innovations. One of the primary innovations produced a secondary gynoecium that developed a fertile innovation, and then again innovated. The other primary innovation soon developed a secondary gynoecium from whose base four innovations proceeded, two associated with each bract. All four innovations formed elongate shoots, three of them sterile, the other producing a tertiary gynoecium with a single elongating innovation! Such strongly ramified female shoots are admittedly exceptional in occurrence.

Differentiation.—*P. sharpii* is allied, among our species, only to *P. semidecurrens* (=*P. alaskana*). It differs from this in the larger leaf cells. Blomquist (1940, p. 94) cites as one of the differences between *P. sharpii* and *"alaskana"* the less spreading leaves of the latter, arranged as to form a smaller angle (*ca.* 45°) with the stem. This, as we have seen, appears to offer no constant means of separation. Perhaps of more significance in separating *P. sharpii* is the leaf-form; this is somewhat ovate, with the apex tapering to a relatively narrow, rounded to subtruncate termination; in *P. alaskana* the leaf varies from suborbicular to somewhat broadly ellipsoidal-ovate, with the apex broadly rounded. Among our eastern species, *P. sharpii* is apt to be confused with *P. asplenioides,* which it considerably overlaps in size. It agrees with the latter in the rather similar leaf-form and numerous marginal teeth of the leaves, in the absence of asexual reproduction, and in the frequent production of sex organs. However, the perceptibly shiny texture when dry and the more olive green to

brown color give *P. sharpii* a different appearance. This is particularly marked when the two species occur together, the *P. asplenioides* being a relatively pure green. Of more importance, *P. sharpii,* under identical conditions, when growing with *P. asplenioides,* has large bulging trigones, while *P. asplenioides* has small and concave-sided trigones.

Culture experiments and study of the plants while growing intermingled in nature show that under identical conditions the two are very different. *P. sharpii,* even in strong shade, has an olive-green to bronzed color, with the stems particularly tending to be brownish; associated plants of *P. asplenioides* are bright green, without any tendency to develop pigmentation. *P. sharpii* has smaller cells, near the margins only 16-18 (23) μ; in *P. asplenioides* they are *ca.* 20-24 x 25-32 μ near the margin of the middle of the postical margin of the leaf (Figs. 9: 1 and 19: 7 were drawn, to the same scale, from two plants, respectively, of *P. sharpii* and *P. asplenioides,* growing side by side, *Schuster* 25007 Whitewater R., North Carolina; the size differences are here clearly evident). *P. sharpii* has the leaves strongly ventrally deflexed along the postical portions of the leaf, with the antical half of the leaf (in xeromorphic forms at least) tending to be suberect; in *P. asplenioides,* the leaves of plants growing under similar conditions spread more distinctly laterally, and the cnemis is much less sharply developed. The median portion of the leaf-base in *P. sharpii* shows strongly elongate cells, averaging 2.5-4 $\times$ as long as wide; in *P. asplenioides* no trace of a vitta is evident, with the median basal cells 20-23 x 32-42 μ, *i.e.,* averaging no more than twice as long as wide. Finally, in living material, the oil-bodies of *P. sharpii* are glistening and clearly homogeneous; those of *P. asplenioides* are clearly segmented.

Among the extraterritorial species, *P. sharpii* appears to be related, according to the investigations of Blomquist (1940) to the Mexican *P. retrosa* Gottsche (De Mexikanske Levermosser, 163-164, Plate XI, 1863), but the latter is a much larger plant, with more extensive denticulation of the leaf. The species also is distantly related to the European Oceanic *P. spinulosa* (Dicks.) Dumort., which has considerably fewer, but more salient marginal teeth of the leaves, larger cells, and is usually not as obviously vittate.

Sectio III. BIDENTES Carl

Plants *small and delicate, often developing brownish pigmentation,* 0.5-2 mm wide. *Branching only intercalary;* aerial leafy shoots rarely branched, except for subfloral innovations. Leaves with a *narrow line of insertion, short-decurrent dorsally, very short-decurrent ventrally;* cnemis poorly developed, the antical margin not to moderately reflexed; leaves widest near or above the middle, *somewhat to distinctly narrowed at base,* obovate to obdeltoid to ellipsoidal-rectangular in form, less than 1.8 X as long as wide, *showing a well-developed tendency to be 1/5-3/5* bilobed, with the accessory teeth usually smaller (or elaborated as linear caducous lobe-like processes). Margins armed with few (0-10) accessory teeth or lobe-like extensions, in addition to the two readily evident primary lobes; *leaf-cells moder-*

ate in size (*ca.* (18) 21-25 x 30-42 μ in leaf-middle), little elongate, *without any trace of basal vitta;* marginal cells not forming a border; *oil-bodies homogeneous, very small, glistening,* rather numerous, usually 8-16 per cell. Stem with cortex bistratose (in species studied), only *ca.* 7-9 cells high. *Underleaves minute and filiform. Reproduction usually entirely asexual,* by means of wholly *caducous leaves, or by caducous teeth or lobes of the leaf.*

Dioecious. Male plants unknown in our species (but known in English *P. tridenticulata*); androecia, where developed, terminal on leading shoots, oblong-clavate, bracts in 4-5 pairs, closely imbricate; bracts "very broad and concave, inciso-dentate at apex, the teeth 2-4, lanceolate-subulate, the antical margin of bract with an additional tooth; antheridia generally solitary, broadly oval, on a pedicel of nearly equal length" (Macvicar, 1926). *Gynoecia terminal on leading shoots,* either regularly without innovations (*P. tridenticulata*) or regularly with 1-2 innovations (*P. caduciloba*); perianth inflated chiefly in the dorsal half of the basal 0.5-0.6, the apical and postical portions compressed; mouth somewhat to distinctly oblique, rounded-truncate, the postical fold ecarinate and nearly to virtually as long as the antical, often more obtuse fold; antical fold not or obsoletely carinulate; mouth pluridentate with remote to hardly contiguous broad-based acuminate teeth, or plurilobate with the lobes contiguous and linear (*P. caduciloba*).

This section is adequately separated from all our other sections by the combination of homogeneous oil-bodies and caducous leaves (or leaf-lobes). It includes the smallest and most delicate of our Plagiochilae, and shows the simplest, smallest stems. In the tendency toward brownish pigmentation and caducous leaves, the group agrees with Sectio IV, the Choachinae or the *P. austini* complex; it differs from it in the smaller size of its species, the homogeneous (*vs.* segmented) oil-bodies, and the fewer marginal teeth of mature leaves. The brownish color and homogeneous oil-bodies suggest Sectio II, the Zonatae, but the resemblance stops there, the latter group reproducing only sexually, having pluridentate, relatively broad leaves that are widest a little above their base in most cases. Among extra-territorial groups, the relationship of the Sectio Bidentes is close to the Spinulosae (*P. spinulosa,* and possibly *P. punctata*). The members of this group (with the two aforementioned species in the oceanic portions of Europe) have homogeneous oil-bodies and show caducous leaves; they have essentially identical-sized cells, and also develop brownish pigmentation. However, the basically different leaf is never deeply bilobed, but ovate-orbicular to ovate, and is provided with sharp spinose marginal teeth.

The two regional species of the Bidentes are not closely allied. In *P. caduciloba* the gynoecia are terminal on leading branches and regularly produce 1-2 innovations; in *P. tridenticulata* gynoecia are similar in position, but never innovate. Both of our species appear to

develop only intercalary branches issuing from the lower ends of the leaf axils. On weak shoots, where the leaves are rudimentary, such branches may occasionally appear postical in origin, but I doubt if they ever truly originate from the narrow ventral merophytes.

The exclusively intercalary branching appears to ally the group to the Choachinae, which possess similar asexual reproductive modes. The regular, if not common, presence of terminal branches in the South African specimen assigned by Arnell (1955) to *P. tridenticulata* at first glance would invalidate these conclusions. However, careful study of the African plant shows conclusively that it is not identical with *P. tridenticulata.* Indeed, the mode of branching suggests it is not even intimately related to it, in spite of the superficial similarities. I have therefore described this species as new, as *P. lophophora* (p. 296), under the discussion of *P. tridenticulata.*

It is also very improbable that the Japanese plants referred by Hattori (1944, 1952) to *P. tridenticulata,* and the Alaskan plants cited by Clark and Frye (1948, 1949) as *P. tridenticulata* bear any affinity to the Bidentes. These plants, although "tending" to be small and to develop incipiently bilobed leaves, have persistent leaves. These plants appear to be small, nearly rhizoid-free phases of *P. rhizophora,* a Japanese species that belongs in the Sectio Subplanae. The separation of this plant from *P. tridenticulata* is dealt with on pp. 295 and 367.

PLAGIOCHILA TRIDENTICULATA (Hook.) Dumort.

Fig. 21

?*Jungermannia spinulosa* var. *b. tridenticulata* Hooker, Brit. Jungerm., pl. 14, figs. 9-10, 1816.

?*Plagiochila tridenticulata* Dumort., Rec. d'Obs. 15, 1835.

Plagiochila exigua Taylor, Trans. Bot. Soc. Edinburgh 1:179, 1843.

Jungermannia exigua Taylor, *ibid.* 1:179, 1843.

Plagiochila tridenticulata Taylor ex Gottsche, Lindenb. & Nees, Syn. Hep. 26, 1844; K. Müller, Rabenh. Krypt.-Fl. 6(1):773, 1911; Macvicar, Studs. Hdb. Brit. Hep. ed. 2:230, figs. 1-3, 1926; K. Müller, Rabenh. Krypt.-Fl. ed. 3, 6:899, fig. 320, 1956.

Plagiochila stableri Pearson, J. Bot., 241, pl. 358, 1896; Hep. Brit. Isl., p. 273, pl. 112, 1900; Macvicar, Studs. Hdb. Brit. Hep. ed. 2:232, figs. 1-6, 1926.

Pedinophyllum stableri K. Müller, Rabenh. Krypt.-Fl. 6(1):780, 1911.

Plants in obscure thin patches or mats, or growing isolated among other Hepaticae (particularly *Bazzania nudicaulis, Anomylia cuneifolia, Frullania tamarisci* subsp. *asagrayana*), pale green to pure green or somewhat olive green, the *stems* ± *brownish.* Shoots mostly *1.0-1.3* (*1.6*) *mm wide,* but plants often persistently juvenile (when epiphytic) and then only 0.7-1.1 mm wide, usually 0.8-2.5 cm long. Stems *filiform and flexuous, wiry and rigid, diffusely monopodially branched;* branches lateral, intercalary, normally issuing at a nearly

right angle from stem, but often *geniculate shortly above origin* (Fig. 21:6) and becoming subparallel or parallel to main shoot. Stems *ca.* 100-120 (135) μ in width when mature, 7-9 cells high, the $\pm$ thick-walled, yellow-brown cortex 1 (-2) cell-layers thick; cortical cells dorsally *ca.* (12) 15-18 (20) μ wide x 12-13 μ thick x (35) 40-70 μ long, thick-walled, $\pm$ brownish; medulla of $\pm$ thick-walled, hyaline cells 15-20 (23) μ in diameter. Rhizoids very infrequent, scattered. Leaves widely spreading, often subtransversely oriented, *remote to approximate,* their line of insertion short (the leaves widest at or shortly above middle in most cases, *distinctly narrowed basally*), somewhat arched but not strongly acroscopically curved; *dorsal leaf-base and ventral leaf-base both characteristically short-decurrent, leaves nearly flat,* the dorsal margin not or hardly reflexed, spreading laterally at an angle of *ca.* 60-85° with stem-apex, *bilobed for ca. 0.2-0.4* (*0.5*) *their length* (most deeply in robust shade forms of wet rocks), the two lobes acute to short acuminate, subequal; leaves *ca.* 225 μ wide x 490-500 μ long to a maximum of 250 μ wide x 800 μ long or 275-400 (420) μ wide x 700-750 (850) μ long, essentially oblong-elliptical to slightly obovate in outline, *distinctly narrowed basally;* leaf-margins entire (xeromorphic extreme) to armed with 1-6 teeth on lobes and distal half of leaf (mesic extreme), one or more of the teeth occasionally large enough to simulate supplementary lobes; dorsal and ventral margins slightly to (usually) rather considerably, and usually nearly equally, arched; sinus from obtuse and deeply lunate (in the shallowly bilobed xeromorphic extreme) to deep and narrow, with acute to narrowly rounded apex (in mesic extremes). Cells distinctly collenchymatous, (18) 20-25 μ subapically, 17-18 (20) μ wide x 30-34 μ long to 21-25 μ wide x 23-30 μ long in the leaf-middle; basal median cells not forming a vitta; marginal cells not or little elongate; *cuticle quite smooth;* trigones (green mesic extremes) very small and concave to (xeric extreme) rather large and distinctly bulging; oil-bodies small, *ca.* 2 x 3.5 μ to 2 x 4 μ, to a maximum of 2.5-3 x 5-6 μ, *glistening, quite homogeneous* (with age rarely obscurely 2-3 transversely segmented), occurring 8-15 per cell; chloroplasts 3.2-4.3 μ, their area equal to slightly less than that of oil-bodies. Underleaves minute, on small shoots often a mere slime papilla, becoming *subulate to filiform and 4-8 cells long, usually uniseriate,* sometimes 2-3 cells broad, tipped by a slime papilla. Asexual reproduction universally present, by *caducous leaves* (*shoots therefore usually very extensively and characteristically denuded, at least with age*).

Male inflorescence on main shoots or branches, becoming intercalary, of 3-5 (6-7) pairs of bracts; perigonal bracts subequal to leaves in size, more transversely inserted and more imbricate, somewhat less spreading (forming a $\pm$ compact spike), often conspicuously fuscous-tinged, as contrasted to the leaves, but bilobed like leaves, and with usually 1-several accessory teeth, one of which is always on antical margin (often above base); antheridium usually solitary. Gynoecia (very rare!) terminal on leading stems, *uniformly lacking innovations*

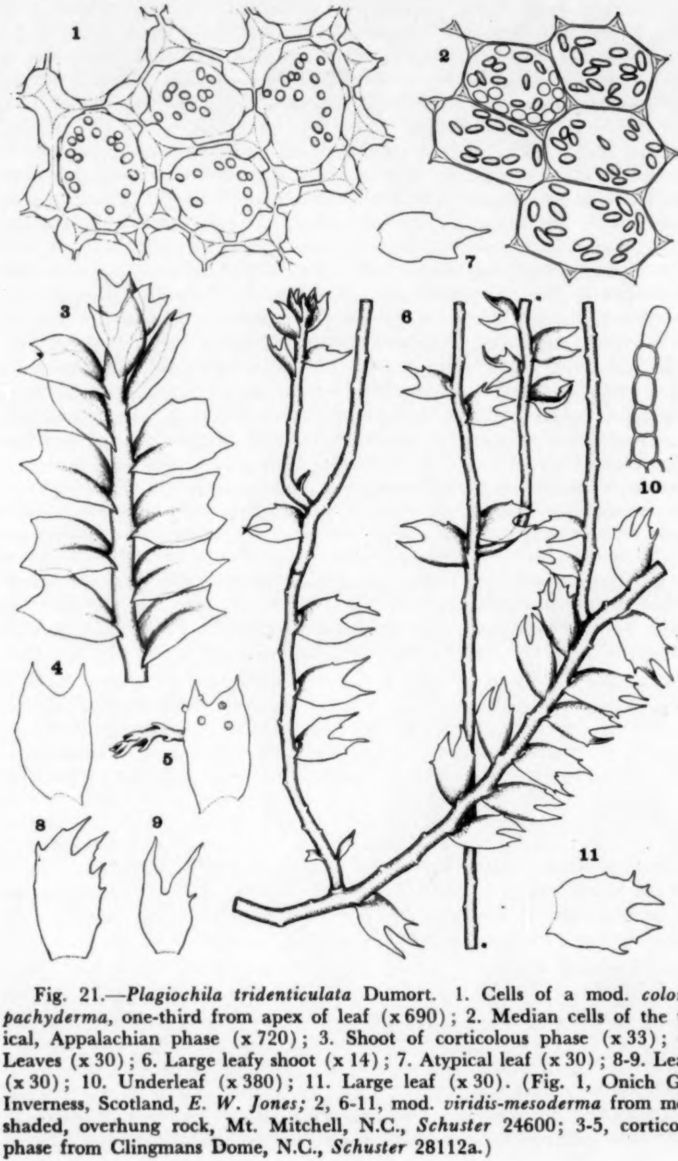

Fig. 21.—*Plagiochila tridenticulata* Dumort. 1. Cells of a mod. *colorata pachyderma,* one-third from apex of leaf (x 690); 2. Median cells of the typical, Appalachian phase (x 720); 3. Shoot of corticolous phase (x 33); 4-5. Leaves (x 30); 6. Large leafy shoot (x 14); 7. Atypical leaf (x 30); 8-9. Leaves (x 30); 10. Underleaf (x 380); 11. Large leaf (x 30). (Fig. 1, Onich Glen, Inverness, Scotland, *E. W. Jones;* 2, 6-11, mod. *viridis-mesoderma* from moist, shaded, overhung rock, Mt. Mitchell, N.C., *Schuster* 24600; 3-5, corticolous phase from Clingmans Dome, N.C., *Schuster* 28112a.)

(even though unfertilized). Bracts polymorphous, erect or suberect, rather remote from perianth, not or hardly sheathing it at base, only slightly larger than the leaves subtending them; often somewhat undulate and postically secund or deflexed, abaxially ± concave, asymmetrically obovate to almost obdeltoid, broadening from a very narrow base upward and widest in or above the middle, the longer and arched antical margin broadly (sometimes weakly) reflexed, the shorter, arched ventral margin often involute, the broad and irregular apical portion *with 3-4 (5) coarse teeth grading into small lobes,* the bract as a whole ranging from (750-850) 1000-1250 μ broad at or above middle x (900) 1500-1600 μ long; at times the bracts more leaf-like, oblong-obovate, only 550-800 μ long x 1100-1350 μ long, the sides weakly arched and nearly subparallel, the oblique apex 3-4-toothed; tooth-like lobes broad-based, varying from triangular and merely acute to short-acuminate and terminated by 2-3 superimposed subisodiametric cells. Perianths (unfertilized) tending to be somewhat postically deflexed, broadly to narrowly obdeltoid to obdeltoid-obcuneate in lateral profile, the antical keel slightly to hardly longer than postical (rarely to 1.5 × as long), the keels fold-like or the antical obscurely ridged near base, *unwinged, the perianth weakly to moderately inflated,* largely in the median portions of the basal one-half, the mouth and distal portions of antical and postical keelar regions strongly laterally compressed; mouth obliquely truncate-rounded, each lip with *11-15 triangular, remote teeth varying greatly in size and shape,* 1-2 larger ones almost lobe-like, the majority spinous from a rather broad base, ending in (1)2-4(5) superimposed single cells 1.5-2 × as long as wide (the terminal often narrower and 2.5-4 × as long as wide).

Type.—The type material of this species is in question. However typified, the type locality is the British Isles.

The nomenclature of this species — and indeed its name — is a matter which needs clarification. The name "*tridenticulata*" goes back to Hooker (1816, pl. 14, figs. 9-10, and text on facing page), who described *Jungermannia spinulosa* var. *b. tridenticulata* as with "foliis minoribus, paucioribus, apicibus trispinosis." His fig. 9 shows a shoot with leaves that are predominantly shallowly trilobed distally, but sometimes bilobed. I have seen no plant of *P. tridenticulata* with a high incidence of tridentate or shallowly trilobate leaves, hence a real question remains as to whether Hooker's "*tridenticulata*" is the same as our present "*tridenticulata.*" Dumortier (1835, p. 15) "elevated" the var. *b* of Hooker to specific rank, as *Plagiochila tridenticulata;* he is, correspondingly, cited as the authority for the species by Frye and Clark (1937-47) and as author of the combination by Joergensen (1934), although the latter clearly places a question mark after the citation, citing "*Plagiochila tridenticulata* (Hook.?) Dumortier?"

The next name published, presumably for the present species, is that of Taylor (1843, Trans. Bot. Soc. Edinburgh 1:179), *Jungermannia* (or *Plagiochila*) *exigua.* The first, clearcut use of *Plagiochila tridenticulata* as a name *for the present species* dates from 1844, when Taylor (*in* Gottsche, Lindenberg and Nees, Synopsis Hepaticarum, p. 26, 1844) published the name. If we

regard the *Plagiochila tridenticulata* of Hooker, and following him Dumortier, as a dubious name, based on a dubious (and perhaps juvenile?) plant, then the first validly published name for the present species is *Plagiochila exigua* Taylor, 1843. (This name is earlier than *P. tridenticulata* Taylor, which was proposed in 1844, *not* in 1838, as Müller [1905-16, and 1956] would have it.)

I would suggest that, since evidence to the contrary is not available, we regard the var. *tridenticulata* of Hooker as identical with *P. tridenticulata* in its modern sense. The type locality is then "mountains near Bantry, Ireland" where it was collected by Miss Hutchins. The other alternative would be to consider *P. tridenticulata* Taylor (1844) a later homonym of the dubious *P. tridenticulata* Dumortier (1835), and to adopt the name *P. exigua* Taylor (1843).

Variation.—Two chief modifications occur in this relatively stenotypic species. On bark, with intermittently moist conditions, we usually find a smaller, more xeromorphic extreme, with less branching (mod. *parvifolia-subintegrifolia-pachyderma-viridis vel colorata*); this has shallower bilobed leaves, with at best 1-2 supplementary teeth on the leaves; has large trigones; is olive-green to somewhat brownish with age. This is the common modification of the species, in North America. More rarely occurs a larger, green robust form, with more deeply bilobed leaves, whose margins are commonly 2-7 dentate (mod. *megafolia-denticulata-fissifolia-leptoderma-viridis*); this modification appears to occur only under extremely shaded conditions (light intensity less than 5 ft.-c.; humidity rarely less than 95%) on wet or damp, overhung rocks or cave-entrances.

In North America, at least, this species generally occurs as a modification with relatively weakly bulging trigones, even on less humid sites on bark (Fig. 21:2). Furthermore, deep brownish pigmentation is rare, or absent, as is indicated in the description. Also, male plants are never encountered. This North American phase is probably different genetically from the British plants on which the species was based. Pearson (1902, p. 280), for example, describes the English plant as "dark indigo-green . . . when dry almost black." Macvicar (1926) also emphasizes the "*nearly black when dry*" [italics his] appearance of the British plant, and states the male inflorescence is "common." In living material, which I owe to E. W. Jones, from Onich Glen, Inverness, Scotland, the plants are male and distinctly fuscous to chestnut brown. The distal halves of the leaves have very coarse trigones (Fig. 21:1), although these are much less pachydermous in the lower halves of the leaves. The oil-bodies in this plant are also smaller (1.3-2 μ long) than in the American plants studied (2 x 3.5-4 to 2.5-3 x 5-6 μ), although this difference may not be significant. For the time being, it seems premature to accord the American plant the status of a separate subspecies, although it may prove, upon repeated, more intensive study, that such separation is deserved.

Distribution.—An oceanic species of great age, with a strongly disjunct distribution limited largely to areas that have not been glaciated, nor submerged, during the last 60,000,000 years or more; found in various temperate Atlantic Islands (Canary Isls.; Azores; Madeira; on the west coast of England, from Wales to West Sutherland; Ireland);

the Norwegian coast; coastal northwest France; the Pyrenees. In North America only in the unglaciated Southern Appalachian Mountains. The reports of the specie from Japan, from the Aleutian Islands, and from South Africa, ai all based on erroneous identifications.

The species is almost restricted to the Red Spruce-Fraser Fir Climax Forest, at elevations from 4800-6800 ft., rarely descending to 4000 ft. into the Mixed Mesophytic Cove Forest.

VIRGINIA: Mt. Rogers (with *Bazzania nudicaulis, Herberta sakuraii;* northernmost station; see Patterson, 1950, p. 39); near summit of Mt. Rogers, *ca.* 5700 ft., Grayson Co. (*Schuster* 38038, 38032, 38032b, with *Herberta sakuraii;* 38032a). NORTH CAROLINA: Mt. Mingus, Swain Co., 5000 ft. (*Sharp* 34703! 34710! with *F. asagrayana, Herberta, Blepharostoma, Lejeunea "patens," Harpalejeunea ovata*); Clingmans Dome, Swain Co., 6500 ft. (*Sharp* 4154!; *Schuster* 28112a 28117b); Andrews Bald, *ca.* 5800 ft., S. of Clingmans Dome, Swain Co. (*Schuster* 39671, *c. per.*, 36600b); Devil's Courthouse, 5500 ft., Transylvania Co. (*Anderson* 11145, 11150!); Mt. Sterling, Haywood Co. (*Blomquist,* June 1933!); Balsam Gap, *ca.* 25 mi. N. of Asheville, along Blue Ridge Parkway, 5220-5260 ft. (*Schuster* 19067, 19087, 19089, 19147, 19080); near SW. summit of Roan Mt., *ca.* 6100 ft., Mitchell Co. (*Schuster* 37969, 36968a); Mt. Mitchell 6200-6700 ft., Yancey Co. (*Schuster* 34203, 34215, 24600a, 24600, 23253, 23269a, 23253a, with *Bazzania nudicaulis, Frullania asagrayana, Herberta sakuraii; Schuster* 23269, with *Anomylia cuneifolia, Bazzania nudicaulis, Frullania asagrayana;* 24608a, with *Anomylia cuneifolia;* 23274a, with *Herberta sakuraii, Tritomaria exsecta, Anomylia cuneifolia,* etc.); Chestnut Bald, 6050 ft., Balsam Mts., SE. of Sunburst, Haywood Co. (*Anderson* 11194, 11191!; the latter on rocks, with *Anomylia cuneifolia, Grimmia apocarpa, Plagiothecium muellerianum*); W. slope of Balsam Cone Mt., Black Mt. Range, 6500 ft., Yancey Co. (*Anderson* 10946!); Richland Balsam Mt., Caney Fork Balsams, SE. of Sylva, Jackson Co., 6400 ft. (*Anderson* 10751!); Devil's Courthouse, Blue Ridge Parkway W. of Wagon Road Gap, Haywood Co., 5500 ft. (*Schuster and Bryan* 39236, 29238); Richland Balsam, E. of Rich Mt. on E. and SE. slopes of summit, 6300-6400 ft., Haywood Co. (*Schuster* 39580, *c. per.!*; 39587, 39621, 39623, 39698a, 39667, 39668); Richland Balsam, on W. and NW. slopes, Jackson Co., 6300-6500 ft. (*Schuster* 39641, 39643, 39600, *c. per.!*); Andrews Bald, SW. of Clingmans Dome, Swain Co., on rocks and bark of *Abies* and *Betula lutea* (*Schuster* 39750, 39751, 39752, *in part c. per.!*). TENNESSEE: Clingmans Dome, Sevier Co., *ca.* 6600 ft. (*Sharp* 5114! 5325!; *Schuster* 34711); Roaring Fork, Sevier Co., *ca.* 6000 ft. (*Sharp,* May 8, 1932); Mt. Le Conte, Sevier Co. (*Sharp* 34977!; *Sharp,* 1935 *in* Verdoorn's Hep. Select. et Crit. No. 478!; *Sharp* 34482!, 35309!); along W. fork of Little Pigeon R., near Chimneys Parking Area, *ca.* 4000 ft., Sevier Co. (*Schuster* 36513); near summit of SW. end of Roan Mt., *ca.* 6200 ft., near N.C. border, Carter Co. (*Schuster* 36941); Appalachian Trail, about 2.5-3 mi. NE. of Newfound Gap, *ca.* 5300 ft. (*Schuster* 41092).

The species has also been reported from Kiushiu Province, Japan (Hattori, Bull. Sci. Mus. Tokyo Univ. No. 11:65, 1944; Hattori, 1952). Dr. Hattori (in litt.) now states this represented an error in determination. I have seen specimens cited in both reports; they represent a form of *P. rhizophora.*

Ecology.—A species of densely shaded, humid forests. In Europe reported from the bark of trees and on rocks (sandstone, etc.). Pre-

viously reported, in this country, only from the bark of *Abies fraseri* at elevations of above 4500 ft. In the dense fog forests of Fraser Fir this species is often frequent, and occurs at 5-10 ft., or higher, on bark. It is associated here with a distinctive group of species, constituting the *Anomylia cuneifolia-Bazzania nudicaulis-Plagiochila tridenticulata* Associule. In addition to the type species, *Frullania asagrayana* is almost constantly consociated, as well as, very frequently, *Lejeunea ulicina* and *Herberta sakuraii* subsp. *tenuis*, occasionally *Cephaloziopsis pearsoni*. Rarely, in similar situations, found on bark of *Betula lutea*.

The consociation with *H. sakuraii*, including its various subspecies is suggestive. Both *H. sakuraii* and *P. tridenticulata* occur in the hyper-oceanic portions of Europe, and recur in the Southern Appalachians, as does *Cephaloziopsis pearsoni*. For a detailed account of the ecology and range of the *Herberta*, see Schuster (1957c); for a similar account of the *Cephaloziopsis*, see Schuster (1959).

With eventual succession, members of the *Lophozia-Scapania* Associule may undergo ecesis in the pioneer *Anomylia-Bazzania-Herberta* Associule, and then *Lepidozia reptans, Blepharostoma trichophyllum, Tritomaria exsecta* and *Anastrophyllum michauxii* become consociated. With the ecesis of these species, the pioneer *Plagiochila tridenticulata* quickly begins to disappear.

In addition to the more frequent occurrences on bark of *Abies fraseri*, the species not infrequently occurs on bark of *Sorbus americana*, where it is associated with *Frullania asagrayana*, rarely *F. oakesiana, Metzgeria fruticulosa*, and occasionally also on *Betula lutea*.

The species is frequent on damp, shaded rocks on several of the highest peaks in the Southern Appalachians. Here it variously occurs with *Lejeunea lamacerina gemminata, Plagiochila sullivantii, Marsupella paroica* (see Schuster, 1957b), *Metzgeria fruticulosa, Cephalozia media, Herberta sakuraii* subsp. *tenuis* (see Schuster, 1957c), *Scapania nemorosa*, etc. Under such conditions the species rarely produces perianths (as in populations on Andrews Bald and on Richland Balsam). I have seen perianths only four times; thrice on material from damp rocks, once (*Schuster* 39600) from the base of *Abies fraseri*. Typical occurrences of this type are those on the summit of Roan Mt. and Mt. Mitchell, N. C. in sites which are overhung by ledges, and further shaded by dense fir forest (light intensity less than 25 f.c.). Under such conditions, the species is associated with members of the extremely shade-tolerating *Diplophyllum taxifolium-Anastrophyllum minutum* facies of the *Lophozia-Scapania Associule* (see Schuster, 1957, p. 267), such as *A. minutum* and *Lepidozia reptans* (as in *Schuster* 24600), occasionally with *Diplophyllum* or *Lejeunea lamacerina;* on more exposed ledges sometimes with *Grimmia apocarpa, Plagiothecium muellerianum* and *Anomylia cuneifolia*.

Differentiation.—Agreeing with several other members of the *Anomylia-Bazzania-Herberta* Associule (specifically *Anomylia cuneifolia, Bazzania nudicaulis*) in the abundant production of caducous leaves. This separates the species from most other North American members of the genus. The small size, distant leaves, and the great polymorphism of the leaves (derived from an essentially 2-lobed leaf)

are further distinctive criteria. Unlike our other species of *Plagiochila,* this species has nearly flat leaves, without the characteristic deflexed antical margin diagnostic of the genus as a whole (Fig. 21: 3,6). The corticolous forms of intermittently moist areas are smaller, usually have shallowly, largely 2, occasionally partly 3-lobed leaves without accessory spinose teeth (Fig. 21:3,4). The forms of very moist rocks (as *Schuster* 24600), once considered distinct as *P. exigua* Tayl., show more deeply, 2-3-lobed leaves usually provided with occasional sharp, spinose accessory teeth or small lobes (Fig. 21: 6-9, 11).

Although *P. tridenticulata* can hardly be confused with any other regional species, it has been widely confused in recent years with a variety of small Plagiochilae with 2-3-lobed leaves. These species include (1) a South African plant, which I must regard as a new species, *P. lophophora,* ascribed by Arnell (1955) to *P. tridenticulata;* (2) an Aleutian plant, reported by Clark and Frye (1948, 1949) from Adak and Attu Islands, as *P. tridenticulata,* evidently represents a race of the polymorphic *P. rhizophora;* similarly, two Japanese reports, by Hattori (1944, 1952) are based not on *P. tridenticulata,* but on a phase of the East Asiatic *P. rhizophora,* as has been pointed out to me by H. Inoue; (3) a South American plant, superficially identical with *P. tridenticulata,* is described below as *P. verruculosa.* It is thus evident that *P. tridenticulata* has been greatly misunderstood in recent years. Hence, the differences from the preceding species appear to need analysis:

(1) **Plagiochila verruculosa,** sp. n.

Plantae minimae, fortiter fuscae, stipites rigidae, filinoides, magnopere sine foliis. Folia frequenter caducosa, generaliter 0.4-0.5 bilobata; mediae cellulae 22-27 μ latitudine; cutem fortiter verruculosum. Typus: Mt. Purace, Cordillera Central, Colombia, *F. W. Pennell and E. P. Killip* 6686.

Entirely similar to *P. tridenticulata* in the very small size, abundantly caducous leaves, usually 2/5-1/2 bilobed leaves, median cells with distinct to bulging trigones that average 22-27 μ wide x 24-28 μ long in the leaf-middle. Differing from *P. tridenticulata* in 1) the strongly brownish coloration of the stems and cell-walls of the vegetative leaves, 2) the even more excessively caducous leaves, resulting largely in filiform, thread-like stems entirely or virtually entirely devoid of leaves, 3) the strongly verruculose cuticle, 4) the strongly striolate, thick-walled and elongate cortical cells of the stem.

Type.—Colombia: Department of El Cauca, "Canaan," Mt. Purace, Cordillera Central, 3100-3300 m, *F. W. Pennell and E. P. Killip* No. 6686. The type specimen is in the New York Botanical Garden, and apparently grew intermixed with *Plagiochila cuneata loriloba* Herzog (of which this collection is also the type). Only a very few plants of *P. cuneata loriloba* are present, but a considerable quantity of *P. verruculosa.*

(2) *Plagiochila rhizophora* Hattori.—The North Pacific plants which have been reported as *P. tridenticulata* all appear to represent

a polymorphic plant only recently distinguished as *P. rhizophora* Hattori (see p. 359). This plant differs from *P. tridenticulata* chiefly in: leaves persistent, rather than caducous; cells larger, averaging usually 25-27, occasionally 28-30 μ wide medially; well-developed stems freely provided with rhizoids; perianth-mouth with numerous small, close, regular teeth (see Hattori, 1950, fig. 57); leaves "tending" to develop more frequent accessory teeth, particularly of the distal half of the postical leaf-margin. The species is, when well-developed, considerably larger than *P. tridenticulata,* attaining a width of 2.5-3.5 mm in extreme cases.

(3) *Plagiochila tridenticulata* also appears clearly, if remotely, allied to a South African plant from Natal, which may be diagnosed as follows:

Plagiochila lophophora, sp. n.

Plantae minimae, virides ad saepissime fuscae, facientes moles intertectas, filiformae stipites aliquam fragiles et rigidae cum siccatae. Similis in aspectu *P. tridenticulatae,* sed terminalibus ramis. Folia brevi-decurrentia in postico, remota ad contigua, oblonga et anguste oblonga-ovata, bifida ca. 0.35-0.4 longitudine, passim cun uno, rariter duabus minoribus auxiliariis dentibus; lobae triangulatae, breviter acuminatae in apice, terminentes 3-4 (5-6) superpositis monocellulis, ultima saepe 2-3 X longa quam lata. Mediae cellulae minimae: 16-18 (19) μ, crassioribus protrudentibus trigonibus; cutem levem. Reproduction asexualis rariter et passim creata caducosis foliis. Typus: Coel Gully, 8000 ft., Injasuti area, Bergville Div., Natal, Africa (*E. Esterhuysen* 26143; July, 1956). Type in herbarium of S. Arnell and of author.

Plants very small, green to (most often) brownish, or at least with stems brownish, forming interwoven, dense mats. Stems filiform, thin and wiry, rather brittle and rigid when dry. Plants similar in aspect to *P. tridenticulata,* but the *stems regularly very acutely, terminally, furcately branched.* Leaves remote to contiguous, short-decurrent postically and moderately decurrent antically, oblong to narrowly oblong-obovate, *bifid for ca.* 0.35-0.4 *their length,* occasionally with 1 or rarely 2 smaller accessory teeth; lobes triangular, short-acuminate at apex, ending in 3-4 (-5-6) superimposed single cells, the terminal one often 2-3 X as long as broad. Median cells very small, 16-18 (19) μ broad, nearly isodiametric, with rather coarse and bulging trigones; *cuticle smooth.* Asexual reproduction rarely and sporadically developed, by means of caducous leaves. Reproductive (sexual) organs unknown.

Type.—Africa: Coel Gully, 8000 ft., Injasuti Area, Bergville Div., Natal (*E. Esterhuysen* 26143; July, 1956). Type (and schizotype) respectively in herbaria of S. Arnell and of author.

This species, superficially, is nearly inseparable from *P. tridenticulata* s. str., and was reported as such by Arnell (1955). However, it

differs in: (a) The interwoven, wiry shoots show free, if remote, development of terminal branches, with the branching in such cases pseudodichotomous; in addition, the older stems show occasional intercalary axillary branches of the "normal" type. (b) The collenchymatous cells are smaller, averaging only 16-18 μ wide medially, with the length not exceeding the width in most cases. (c) The leaf-lobes are short-acuminate in all cases, ending in a tapering cilium (3)4-5(6) cells long, whose terminal cells are commonly 2-3 times as long as wide. (d) The leaves appear to be persistent or at least only rarely and tardily caducous. (e) The underleaves are very distinct and elongate, although filiform or ciliiform in shape.

In true *P. tridenticulata* I have searched repeatedly for evidence of terminal branching, without success. Both English material (Onich Glen, Inverness, Scotland, *E. W. Jones*) and a suite of Appalachian plants have been examined, without a single unquestionable terminal branch being found. Müller (1942) has also shown that *P. tridenticulata* has very characteristic intercalary branching, with the branches often geniculate near the base. The leaf-cells of true *P. tridenticulata,* although variable, do not range as small in size as those of *P. lophophora.* In the British plants seen they range about 19-23 μ wide x 20-25 μ long; in American plants, usually 18-21 x 22-25 to 20-23 x 20-26 μ. Although the leaf-lobes of true *P. tridenticulata* may be similarly pointed, this is infrequently the case. Finally, true *P. tridenticulata* rarely shows as elongate and conspicuous underleaves.

The branching modes in *P. lophophora* are of the utmost interest. In addition to the primary mode of terminal branching, two other types of branches are to be seen. The furcate terminal branches typically diverge at a very narrow angle, usually *ca.* 20-25, rarely 30 degrees; the branch is equal in vigor usually to the continuing main axis, and the position of the branch is recognizable only because it is subtended by a lanceolate and short-acuminate to longly acute supporting leaf. The older portions of the plants also periodically, if sporadically, may produce wide-spreading (65-75° usually, rarely only 45°) lateral intercalary branches, some of which may branch again by terminal branching. In addition, at least one leafy branch was seen of unquestionably postical origin, arising from the axil of the filiform underleaf. Such postical branches are of rare and sporadic occurrence in *Plagiochila.*

In spite of the great habitual similarity then, *P. lophophora* may readily be separated from *P. tridenticulata* by the regular occurrence of terminal branching. The smooth cuticle, as well as branching modes, serve to separate the species from *P. verruculosa.* These three species, and small forms of *P. rhizophora* are superficially identical and similar in size; they are separable by the following key:

1. Plants with cuticle smooth. 2
   2. Branching totally intercalary, the branches all arising from the axils of leaves and typically geniculate a short distance above their origin; cells usually 20-27 (30) μ wide on mature leaves; underleaves vestigial, usually only 4-5 (6) cells long. Northern Hemisphere. 3

3. Leaves freely caducous; median cells (17) 20-25 μ wide; leaves dorsally short-decurrent; mature plants very sparsely rhizoidous. Peripheral to North Atlantic. .... *P. tridenticulata*
3. Leaves persistent; median cells 25-27 (28-30) μ wide; leaves dorsally long-decurrent; mature plants densely rhizoidous. Peripheral to North Pacific. .... *P. rhizophora*

2. Branching regularly acutely furcate and terminal, the branch subtended by an unlobed, narrow, lanceolate leaf; in addition with sporadic lateral and postical intercalary branches; cells usually 16-19 μ wide on mature leaves; underleaves ciliiform, of a uniseriate cilium up to 6-7 (8) cells long, with usually 1-2 shorter cilia at base; leaves long-decurrent dorsally. South Africa. .... *P. lophophora*

1. Plants with cuticle closely verruculose; neotropical. *P. verruculosa*

PLAGIOCHILA CADUCILOBA Blomquist

Figs. 22-23

Plagiochila caduciloba Blomquist, The Bryologist 42:114, 1939.
Plagiochila sullivantii Evans (*nec* Gottsche), The Bryologist, 18:82, 1915.

Plants with distinct differentiation into creeping stoloniferous shoot system, and aerial branches at nearly right angles from the substrate (which is normally the undersurface of projecting ledges or nearly vertical rock-walls, rarely, shaded damp bark). Plants usually dull olive-green, in dense shade pure green, but even with diffuse sunlight *becoming strongly brownish-pigmented.* Aerial leafy shoots characteristically simple, rarely with a single branch, usually 0.8-1.8 (rarely 2-2.5) cm long, usually in diffuse patches (the aerial stems usually distinctly, often widely separated); shoots with the nearly straight stems rather brittle and stiff, with the leaves (0.8) 1.1-1.8, rarely 2 mm wide. *Stems brownish, ca.* 120-160, occasionally 180 μ in diameter; cortical stem cells in two layers, thick-walled, narrowly oblong, scarcely tangentially flattened, 12-16 (18) x 36-60 μ, mostly 3-5 X as long as wide, somewhat shorter and narrower than the thin-walled medullary cells; medullary cells mostly in 4-5 cell-layers (stem thus *ca.* 8 cells high), very elongate. Rhizoids very infrequent or absent on aerial shoots. Leaves distant to approximate, usually characteristically dorsally convex, the distal portions of the leaf somewhat decurved, the antical margin scarcely to slightly decurved (cnemis obsolete to relatively poorly developed), *inserted by a narrow line* that is moderately curved and somewhat acroscopically arched; *leaves essentially obovate or obdeltoid in outline,* sometimes narrowly so, when young (before fragmentation) *ca.* 1.2-1.4X as long as wide, *ca.* 1-1.35 mm long x 0.8-1.0 mm wide, slightly to barely decurrent postically, shortly decurrent dorsally, erect-spreading (never strongly laterally spreading), at an angle of *ca.* 45-60 degrees with stem; antical and postical margins both nearly straight, divergent, both somewhat reflexed (the postical often more strongly so), with unlobed basal part of the leaf consequently more or less strongly adaxially convex, lobate apical region usually decurved; apex of leaves essentially truncate to

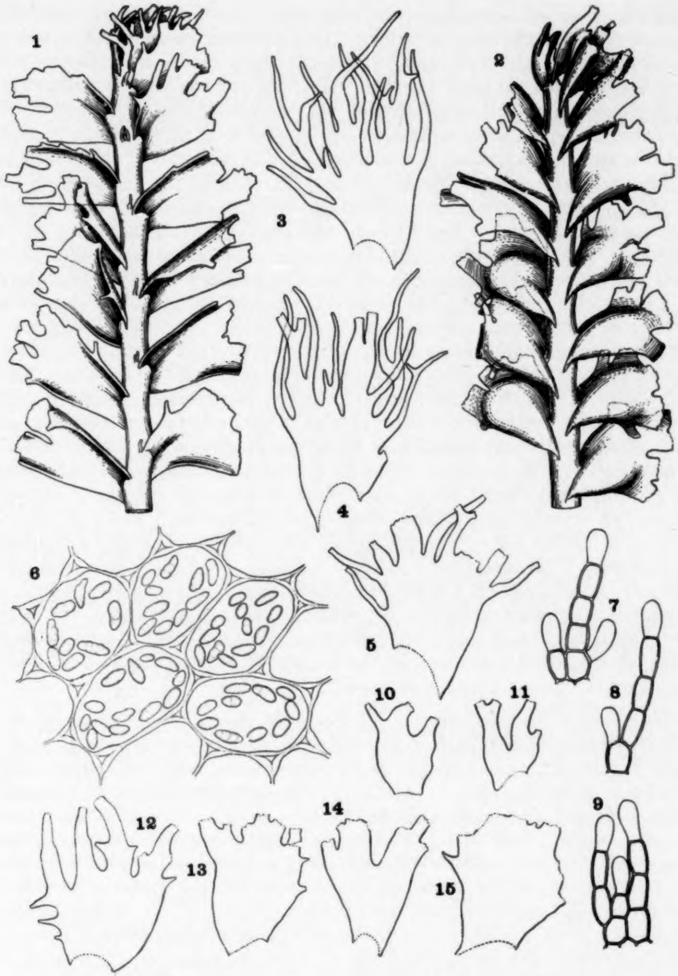

Fig. 22.—*Plagiochila caduciloba* Blomquist. 1-2. Postical and antical aspects of shoots, small, xeromorphic mod. *parvifolia-colorata* (x 34); 3-5. Leaves, in series from shoot apex back, mod. *viridis-megafolia* (x 26); 6. Median cells with oil-bodies (x 450); 7-9. Underleaves (x 210); 10-11. Small, juvenile leaves (x 34); 12-15. Leaves, showing progressive fragmentation (x 25). (Figs. 1-2, 7-9, Tallulah Falls, Georgia, *Small* 9309; 3-5, 10-11, Dry Falls, N.C., *Schuster;* 6. Whitewater Gorge, N.C., *Schuster* 25003; 12-15, from type specimen.)

truncate-rounded (ignoring the incisions), the margins below the incised distal half usually entire (or the often somewhat revolute postical margin with 1-3 teeth); distal 1/2-3/5 of the leaf bilobed, the two *major lobes usually bearing 4-5 long linear lobes, or attenuate teeth,* some of which may bear 1-2 shorter tertiary lobes or teeth, *the luxuriant lobing thus quite polymorphic and irregular;* in other cases, the two primary lobes soon dividing into 2-3 secondary lobes, each of which may bear several linear ultimate lobes; small branch leaves *ca.* 320-350 μ long, bilobed or occasionally trilobed, the lobes not or only occasionally divided. Leaves, on or shortly before attaining their definitive size, with the ultimate *lobes fragmenting and caducous;* with age, the process of fragmentation continuing until the secondary, and even the primary lobes gradually breaking up into fragments, *leaving an irregularly truncate, obcuneate leaf* (usually showing some vestige of the primary sinus as an interruption of the irregularly truncate apex). Cells of leaf-middle more or less collenchymatous, and with bulging, large trigones and thickened intervening walls (except in green leptodermous extremes), the trigones between longitudinal walls often confluent; apical cells 21-25 μ; median cells 20-25 x 32-42 μ, near base 25-28 μ wide and to 45 μ long: the basal cells not forming a vitta; oil-bodies 9-14 per cell, more or less fusiform, drop-like, or ellipsoidal, *smooth and homogeneous, glistening, ca.* 3 x 4-5 μ to 4 x 6-7.5 μ, a few to 3-4 x 9 μ, the larger with age occasionally obscurely transversely 2-5-segmented; cuticle smooth. Underleaves minute, subulate, consisting of 1-2 rows of cells near or at base, uniseriate throughout or sometimes of 2-3 short, capillary segments 2-4 cells long (each with terminal cell ending in a slime papilla), 100-125 μ long. *Asexual reproduction by fragmentation of the linear leaf-lobes* (as above).

Dioecious. Female organs very rarely developed. Gynoecia on leading shoots, either with one subfloral innovation (which may be again fertile), then becoming pseudolateral, or with two sterile innovations, then situated in notch of dichotomy; *innovations arising between bracts and perianth.* Bracts very similar to leaves in shape and size, usually 900-950 (1050-1150) μ long (before dehiscence of lobes) x 525-575 (700-850) μ broad, asymmetrically and broadly obcuneate to obovate, 2-4-lobed to the middle, the lobes subdivided into linear filiform caducous teeth, the antical margin rather longly decurrent, weakly deflexed near base; bracts eventually narrowly obdeltoid-obcuneate and irregularly truncate at apex; bracts obliquely patent, nearly horizontally so, not at all sheathing perianth. Perianths (unfertilized archegonial stage) narrowly ovoid in dorsal view (650-950) 1200-1450 μ long x (400) 600-820 μ maximal subapical width, in lateral view broadly obdeltoid-obcuneate, at the mouth wide and rounded-truncate to truncate, *divided into numerous small lobes which bear* 28-35 linear teeth, to 200-450 μ long, often 1-2 dentate marginally, that are 1-2 cells wide; the teeth (2-3) 5-10 (12-22) cells long, the distal 2-12 (15) cells forming a uniseriate row, the *teeth tardily but*

freely caducous; perianths with antical and postical keels obtuse and hardly distinct, *subequal in length, without trace of wings,* or the postical keel shorter (rarely obsolete) and acutely folded although ecarinate.

Type.—Greenbrier, Sevier Co., Smoky Mts. Natl. Park, Tennessee (*Sharp* 3871! *UT, DU!*).

Distribution.—A very local, but locally frequent species, confined almost exclusively to cascading mountain streams and ravines, largely to the *Leucothöe editorum-Rhododendron maximum* Association along the margins of streams, in the Mixed Mesophytic Cove Forest of the Southern Appalachians, associated typically with *Liriodendron, Magnolia fraseri, Calycanthus, Tsuga canadensis, Halesia caroliniana,* etc. Largely at 2500-4000 ft., thus occurring almost wholly below the Spruce-Fir Zone, but descending in the gorges occasionally to 1000-1200 ft., along the Escarpment Region; rarely upward into the Spruce-Fir Zone (to 6050 ft.).

NORTH CAROLINA: Whitewater River gorge, Jackson Co. (*Anderson* 6638, 6641, 8753, *Schuster* 25019, 25008, 34735a, 34737, with *P. virginica* var. *caroliniana*); Dry Falls, *ca.* 3 mi. NW. of Highlands, on Route 64, Macon Co. (*Schuster* 25227, 25243, 25254, 25257, 25217, 36506c); below Rainbow Falls, S. of Oakland, edge of stream-bed of Horsepasture River, *ca.* 2520 ft., Transylvania Co. (*Schuster* 34725); below High Falls of Whitewater R., Transylvania Co. (*Schuster* 25004, 40571); Linville River Gorge, below falls, Burke Co. (*Schuster and Jones* 28952, 29469); Buck Creek, W. of Black Gap, *ca.* 3200 ft., along Route 64, Clay Co. (*Schuster* 38203); escarpment gorge of Toxaway Creek, off Toxaway Gorge, 8 mi. SW. of Rosman, Transylvania Co., 1200 ft. (*Anderson* 11087!); Thompson R. gorge, 4 mi. SE. of Bohaynee, Transylvania Co. (*Anderson* 11103!); Bearwallow Falls, Toxaway Gorge, Transylvania Co. (*Anderson* 4295!); Trays Island Cr. under Bald Rock Mt., 3.5 mi. W. of Cashiers, Jackson Co. (*Anderson* 10257!); Big Dog Mt., above Dry Falls, near Highlands, Macon Co. (*Anderson* 9102!); below Windy Falls, Horsepasture R., Transylvania Co. (*Anderson* 8473!); Barnett Cr., below Perry Gap, Shooting Creek, Clay Co., 3700 ft. (*Anderson* 8019!); Spruce-fir zone (6050 ft.), Chestnut Bald SE. of Sunburst, Caney Fork Balsams, Transylvania Co. (*Anderson* 11170!); Chattooga R., *ca.* 0.7 mi. below the Narrows, near bridge, *ca.* 1 mi. N. of Georgia line, Jackson Co. (*Schuster* 39810, *p.p.*; with *Lophocolea muricata*); Narrows of the Chattooga R., *ca.* 2500 ft., east side, under overhanging ledges, Jackson Co. (*Schuster* 39412, 39412a, *c. per.!*); W. Branch from Fork Ridge, of W. Fork Pigeon R., above jct. with Flat Laurel Cr., 4500 ft., Haywood Co. (*Schuster and Bryan* 39261); Chattooga R., east side, 0.2 mi. N. of Ellicott Rock (N. of Georgia-South Carolina state lines), 2000-2100 ft. (*Schuster and Bryan* 39182, *c. per.!*); Toxaway Creek, 0.2-0.3 mi. above confluence with Toxaway River, 1000-1200 ft., Transylvania Co. (*Schuster and L. E. Anderson* 40102, 40130, *p.p.!* in part with *Diphyscium cumberlandianum*); Cullasaja Falls, NW. of Highlands, Macon Co. (*Taylor* 2200!, 2207!, 2205!); Whitewater R. gorge, *ca.* 0.5-0.8 mi. below High Falls, very close to S. C. line, Jackson Co. (*Schuster* 40551a, with *Lophocolea muricata,* etc.); Glenn Falls, SW. of Highlands, Macon Co., above the Falls, *ca.* 3500 ft., in small quantity (*Schuster* 40604, *p.p.,* with gametophyte

of *Hymenophyllum* and *Radula sullivantii*). TENNESSEE: Moist bluff along creek from Spruce Flats below Tremont, Blount Co. (*Sharp and Wells* 543!); along creek from Spruce Flats, running into middle prong of Little River, below Tremont, Blount Co. (*Schuster and Sharp* 34623, 34632, 34641; 34621, with *P. austini*); along West fork of Little Pigeon River, near Chimneys Parking Lot, *ca.* 4000 ft., Sevier Co. (*Schuster* 36535, 36535a, 36535b, 36535c); yellow birch bark, Chimneys Parking Lot, Sevier Co., 3500 ft. (*Sharp* 4125!; with *R. obconica*); East prong of river, Greenbrier, Sevier Co. (*Sharp* 3871, *TYPE*); Pinnacle Trail, Greenbrier, Sevier Co. (*Sharp* 341101!); Bullhead, Mt. Leconte, Sevier Co. (*Sharp* 341028); Blount Co., Spruce Falls Branch, Tremont (*Sharp* 34205!, 34603!). SOUTH CAROLINA: Gorge of Whitewater River, 4-5 mi. NW. of Jocassee, Oconee Co. (*Schuster* 25163, 25169); first large western tributary of Whitewater R., south of N.C. border, Oconee Co. (*Schuster* 38381); E. side of Chattooga River, 0.3-0.8 mi. S. of Ellicott Rock, 1900-2000 ft., Oconee Co. (*Schuster and V. Bryan* 39902, 39903); Gorge of Thompson R., about 1.5-2 mi. above jct. with Whitewater R., N. of Jocassee, Oconee Co. (*Schuster* 41011). GEORGIA: Cañon at Tallulah Falls, 1400-1600 ft., April, 1893 (*J. K. Small* 9309!, 9311!, 9314!); these specimens, in the New York Botanical Garden, were determined by A. W. Evans as *P. sullivantii* and were the basis for the report (Evans, 1915) of the species from Georgia. W. side of Chattooga River, SW. of Ellicott Rock, barely inside Rabun Co., 2000 ft. (*Schuster and V. Bryan* 39834 *c. per.*, 39831, 39860, 39869a, 39870a, and 39835 *p. p.* with *P. asplenioides, P. sharpii, P. sullivantii, Radula obconica* and *Lophocolea muricata;* the species here barely but definitely penetrating southward into Georgia, dropping out along the Chattooga R. within 0.2-0.3 mi. of the N. C. border); damp overhanging ledges on S. side of High Falls of Big Creek, 4 mi. SSE. of Highlands, *ca.* 0.2 mi. S. of the North Carolina border, in Rabun Co., 1900-2000 ft. (*Schuster and H. Wright* 39941, 39956); vertical sides of large boulders in ravine of Big Creek, *ca.* 0.2-0.3 mi. below High Falls (*Schuster* 40021, *c. per., p. p.,* with *Tritomaria exsecta, Plagiochila sharpii*); bark of *Rhododendron maximum,* gorge of Big Creek below High Falls, *ca.* 1800-1900 ft., Rabun Co. (*Schuster* 40689a).

Ecology:—Essentially restricted to shaded, damp rock-faces, almost invariably at or near the edges of cascading streams, or near waterfalls; *e.g.,* in areas of exceedingly high humidity, often near (but never in) the spray zone, with no direct sunlight. Less frequently the species occurs on the bark of trees at such sites, as at Buck Creek, west of Black Gap, *ca.* 3200 ft., on Route 64, Clay Co., N. C. (*Schuster* 38203), and on a large yellow birch in the gorge of the Whitewater R. (*Schuster* 40571); at the latter site associated with *Plagiochila sharpii, Lejeunea laetevirens, L. ruthii, Radula obconica* and *Leucolejeunea clypeata.* The corticolous phases may form dense tufts as high as 6-12 ft. above ground level; the individual plants are usually small and rarely exceed 8-10 mm in height. The species is particularly frequent on bark in the gorge of Big Creek, Georgia (*Schuster* 40689a) where the humidity is apparently exceptionally high. Here it is found on *Rhododendron maximum,* sometimes *R. punctatum,* associated with *Radula obconica* and *Lejeunea ruthii,* as a slender, reduced phase. The plants have unbranched aerial shoots, often only 650-800 μ wide; the leaves are narrowly oblong-obcuneate and variously

bifid for 0.6-0.7 their length, the lobes linear, or else trifid, with occasional development of accessory lobes, leading to the development of characteristic, staghorn-like branching. Such persistently juvenile phases closely approach *P. cuneata* var. *loriloba.* The populations on bark are certainly dependent on a reservoir population of nearby rock faces.

In spite of the shaded, damp habitat, the plants at maturity are apparently always olive-green or bronzed to brownish, often a clear castaneous brown; rarely (as at Dry Falls) plants occur on the overhung rock near waterfalls in exceptionally moist and shaded sites, and there we find that brownish pigmentation is not developed. Such modifications (mod. *viridis-leptoderma*) are exceedingly rare.

Although the species is locally distributed, where it does occur it is often one of the most common hepatics (as in the Whitewater R. gorge). It is associated most often with several other *Plagiochila* species (*P. sharpii, P. virginica caroliniana, P. yokogurensis fragilifolia*), as in the Whitewater R. gorge or *P. austini* (as at Dry Falls), with *Herberta sakuraii tenuis, Blepharostoma trichophyllum, Lejeunea lamacerina gemminata, Harpalejeunea ovata,* occasionally *Radula tenax* or *obconica.* In the gorge of the Linville River it occurs in overhung, deeply shaded recesses under vertical cliffs, under conditions identical to those where *P. austini* and *sullivantii* occur. The plants are found admixed occasionally with *Radula tenax,* and occur closely adjacent to moister sites frequented by *Metzgeria hamata* and the moss *Hookeria acutifolia.* The distribution indicates that the species "avoids" limestone. It is essentially a montane and submontane endemic of the Southern Appalachian Mountains, occurring at elevations between 1400-4000 ft., rarely extending into the Spruce-Fir zone at over 6000 ft.

At the southernmost and altitudinally, the lowest of its occurrences, between 1800-2000 ft., the species occurs occasionally with the rare *Lophocolea muricata.* This is the case, for example, along the Chattooga R., where it is found on rocks with *Plagiochila sharpii, P. asplenioides, Radula obconica* and various mosses. It also occurs in the Whitewater R., as a small, highly reduced form on the bark of Yellow Birch, together with *Lophocolea muricata,* and with traces of *Plagiochila sharpii,* as well as *Lejeunea ruthii, L. laetevirens, Harpalejeunea ovata, Radula tenax,* and *R. obconica, Bazzania trilobata* and a species of *Plagiothecium.*

The saxicolous phases of *P. caduciloba* frequently occur in deep, wet recesses (where they are usually confined, however, to the underside of projecting ledges), in very dense shade. Under such conditions *Radula sullivantii* and *Hookeria acutifolia* are often admixed. Also associated is an undescribed *Calypogeia* (allied to *C. muelleriana,* but with chromosome No. $n = 9$) and an undescribed, gemmiparous fern gametophyte probably belonging to the genus *Hymenophyllum.* The association with the latter plant is a particularly constant one.

Variation.—Although *P. caduciloba* may simply represent a singu-

lar endemic subspecies of a wide ranging neotropical, polytypic species, *P. cuneata,* the regional material exhibits relatively limited variation. Under the most exposed and least mesic conditions, the plants may exhibit a clear golden chestnut-brown pigmentation (often deeper than in the frequently associated *P. austini* and *sullivantii,* with which this modification occurs at Dry Falls, N. C.) and the cells then are thick-walled, with large, often somewhat confluent trigones. This modification has relatively few elongate leaves and the plants are small (in the extreme, deeply brownish-tinged material from Tallulah

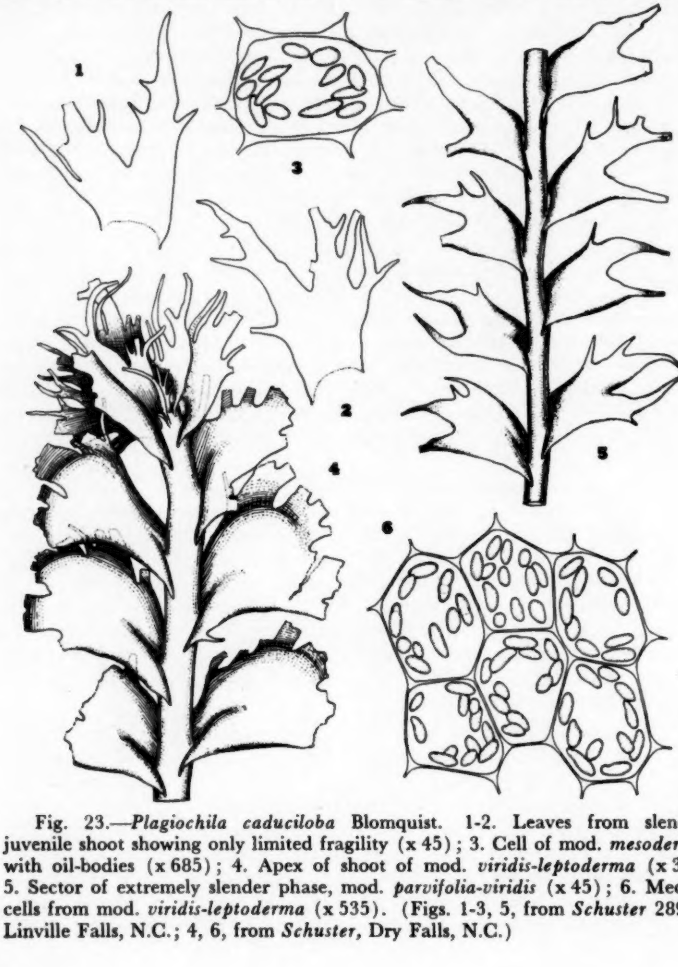

Fig. 23.—*Plagiochila caduciloba* Blomquist. 1-2. Leaves from slender, juvenile shoot showing only limited fragility (x 45); 3. Cell of mod. *mesoderma,* with oil-bodies (x 685); 4. Apex of shoot of mod. *viridis-leptoderma* (x 35); 5. Sector of extremely slender phase, mod. *parvifolia-viridis* (x 45); 6. Median cells from mod. *viridis-leptoderma* (x 535). (Figs. 1-3, 5, from *Schuster* 28952, Linville Falls, N.C.; 4, 6, from *Schuster,* Dry Falls, N.C.)

Falls only 1-1.2 mm wide); it represents the mod. *colorata-pachyderma.* It has the leaves much more suberect, and more strongly adaxially convex than the hygric extreme (Fig. 22:2). Under the most deeply shaded conditions the plant becomes olive-green or even clear green, and then shows small, concave trigones (Fig. 23:6); the leaves of this modification may be more elongate and larger (1.35-1.5 mm long in extreme cases), divided 3/5 their length or even deeper, more luxuriantly divided, and may even approach "var." *loriloba* of *P. cuneata,* even though the leaves are still less elongate; such plants represent the mod. *viridis-leptoderma-fissifolia* (Fig. 22:3-4 illustrates complete leaves of this form).

In addition to this variation in leaf-form and orientation, we find that the species often occurs as slender, extremely distant-leaved forms only 1-1.2 mm wide, in areas of excessive shade. Such plants are of particular interest in that they show more clearly what the ancestral form of the species probably looked like than any other phase of the species which the writer has found. A good example of plants of this type are those collected by the writer below Linville Falls, N. C. (*Schuster* 28952). Here many plants show slender stems, *ca.* 80 μ in diameter, and are only 1 mm wide (Fig. 23:5). The leaves show reversion to the putative ancestral condition. They are bilobed for about one-half their length, with narrow, attenuate lobes; the postical margin bears 1-2 spiniform teeth, or occasionally is edentate, the antical margin occasionally bears a sharp tooth. The teeth, though variable in size, agree in being narrow-based and only 1-2 cells wide x 3-6 cells long; they are not or rarely caducous. The two chief lobes, however, are caducous distally. If shoots of this type (Fig. 23:5) are compared with *P. tridenticulata* (Fig. 21:6) the relationship between the two species is self-evident, and the original suggestions regarding its affiliation (Blomquist, 1939) are clearly shown to have been correct.

Asexual Reproduction.—It is difficult to obtain any idea of the normal leaf-form in this species, since the leaves, attaining their mature size, undergo fragmentation; the lobes break into fragments which are only 3-4 cells large, in others as many as 30-50 cells in extent. These fragments serve as the sole known reproductive mechanism of the species. The leaf, shortly before undergoing fragmentation is portrayed in Figure 22:3-4; it is evident that such leaves are basically bilobed, with each lobe resolved into 4-6 or even 8-9 cilia, which vary from 1-2 to occasionally 3-4 cells wide. These cilia evidently represent a modification of the marginal spinose teeth of the leaves of "normal" *Plagiochila* species as is evident from studying juvenile forms of the species (Fig. 23:5). Fragmentation of the leaves generally first involves the distal portions of the cilia, as is evident from Fig. 22:4-5; subsequently the basal portions of the narrower cilia break off leaving stumps of the secondary lobes that vary from 2-6 cells wide. Fragmentation, as is evident under the microscope, is the result of dissolution of the substances of the middle lamella, since each fragment has complete cell-walls at the "broken" ends. The ends of the "stubs" left on the leaves at this point are therefore quite irregular, since the line of dehiscence follows an angular, jagged line corresponding to the irregular cell-orientation. Finally at maturity, the "stumps" of the secondary lobes, and

even the bases of the primary two lobes drop away, resulting in the typically irregularly, broadly obcuneate leaf that characterizes this species. The exceeding delicacy of the leaves is readily evident from Fig. 23:4, where we can see that fragmentation is virtually completed in 4-5 leaf-pairs from the apex.

Differentiation.—One of the most easily recognized and strikingly distinct species of *Plagiochila*. The size of the plant (to 1.2-1.8 mm wide), the frequently brownish pigmentation, and the essentially obovate to obelliptic leaf-shape give the species the superficial appearance of a form of *P. sullivantii* with the leaf-lobes broken off. The ragged leaves, with truncated, broken-off lobes, the larger trigones of the cells, and tendency for the cell-walls to become thickened between the trigones at once separate the species from *P. sullivantii*. It should be noted that in *P. sullivantii* the entire leaf may be caducous—but the spinous marginal teeth are always persistent. The species should not be confused with any other hepatic, since this is our only species with freely caducous leaf-lobes.

The plants are almost invariably a transparent chestnut brown, occasionally in unduly exposed sites becoming deep brown. Only the *P. austini-sullivantii* complex usually bears a similar color. When living plants are available, the oil-bodies are highly diagnostic: they are glistening, ellipsoidal to fusiform, and quite homogeneous (rarely, a few develop with age slight segmentation into 3-5 segments). Only *P. sharpii* and *tridenticulata*, of our other species, bear such homogeneous oil-bodies.

Normal modifications of the species are also recognizable on the basis of the larger cells (21-25, occasionally 30 μ wide x 28-38, occasionally 42 μ long), which separate the species at once from our other species with homogeneous oil-bodies (*P. sharpii*) and the large trigones of both median and marginal cells (in *P. sharpii* the marginal cells usually forming a thick-walled border).

The plants of normal forms (mod. *colorata-pachyderma*) are also usually characteristically decurved-leaved, especially in drying. When moist, the leaves still tend to be somewhat decurved, and are usually rather distinctly dorsally convex (adaxially convex), with postical margin strongly and antical margin weakly deflexed or recurved. The small size of the plants is also very typical: average shoots are 1.2-1.5 mm wide, which eliminates all but the smallest forms of *P. sullivantii* and the equally small, or smaller, *P. tridenticulata*.

Young leaves, at the shoot apices, are usually distinctly bifid, with the two main lobes again often bilobed (resulting in a palmately 4-lobed leaf), or irregularly provided with narrowly lingulate supplementary lobes; in addition, the lower margins of the leaf may each bear 1-2 small (1-3 celled) subacute teeth. In no case does the mature leaf bear spinose marginal teeth, although juvenile leaves may do so. As the leaves mature the more or less linear to lingulate leaf-lobes begin to fragment into small sections and drop off. For that reason, it is usual to find the shoot apex with the few clustered juvenile apical leaves appearing longly lobed or laciniately divided, while the mature leaves are mere irregular, often raggedly obcuneate structures that bear no resem-

blance to the normal plagiochiloid leaf. I have carefully compared the type of *P. caduciloba* with that of *P. cuneata* var. *loriloba* Herz. (from Columbia). Blomquist (1939, p. 117), in comparing his *P. caduciloba* to *P. cuneata* states that "*P. cuneata* does not, however, show a strong irregularity in secondary lobing nor any extreme tendency to an early shedding of the lobes." In *P. cuneata* var. *loriloba,* judging from the 4-5 stems of the type I have studied, the leaves actually do not appear to show the strong tendency of *P. caduciloba* to form numerous supplementary or accessory lobes, but they do show the early tendency for the leaves to fragment. I was unable to find entire leaves, except in the "apical bud" where immature leaves show the same tendency to form long, linear to lingulate lobes (as in *P. caduciloba*). In *P. cuneata* var. *loriloba* I did find that the cells often tend to be larger (up to 25-32 μ wide in the leaf-middle, on an average, *vs.* 21-25 μ in *P. caduciloba*). The writer suggests that further study may show that *P. caduciloba* may be considered a subspecies of *P. cuneata.* The close affinity of the two taxa is sharply demonstrated by some of the plants of *P. caduciloba* collected by Anderson at unusually high elevations (6050 ft.) in North Carolina. In these plants the leaves are predominantly 2-3-lobed, with few or no accessory lobes!

P. caduciloba also shows a distinct relationship to *P. tridenticulata,* as is evident from the cell-size, the homogeneous oil-bodies, the basic leaf-form (narrow-based), and the small size (less than 2 mm wide). Although this relationship is totally obscured by the extraordinary prolongation of the teeth of the leaves into filiform, fragile lobes (in *P. caduciloba*), careful study of juvenile plants shows that the relationship does exist. The plants of *Schuster* 28952 (Linville Gorge) show this clearly. Small plants are 1 mm wide (width of mature *P. tridenticulata*), and show narrow bilobed leaves bearing 0-3, rarely 4 small spinose supplementary teeth; the teeth are not or barely caducous, but the lobes show a greater tendency to fragment. Except for this, such juvenile plants might be taken for a form of *P. tridenticulata.* (Compare Figs. 21:6 and 23:5). The nature of the asexual reproductive pattern at once suffices to separate these two species, as well as the basically obdeltoid leaf-form of *P. caduciloba.*

The female plants of *P. caduciloba* differ markedly from the female plants of *P. tridenticulata* in a number of respects. There are almost constantly 1 or 2 subfloral innovations in the former; in *P. tridenticulata* they are lacking. The perianth-mouth of *P. caduciloba* is armed with irregular lobes and linear, tardily caducous teeth, exactly as are the distal portions of the leaves; in *P. tridenticulata* the perianth mouth is irregularly toothed with sparing triangular to acute teeth of variable size.

P. caduciloba apparently rarely produces perianths and never appears to produce androecia. Evidently only female plants occur. The perianths are terminated much like the leaves, bearing numerous linear, sometimes branched or dentate teeth and small narrow lobes that are caducous with age, at least in part. Unlike the leaves, the tendency to fragment is not as strongly developed and seems restricted to the distal portions of the longer teeth. The rather stout, in antical aspect, ovoid form of the perianth, with the antical keel essentially

absent is characteristic. The nearly constant occurrence of 1, or more often 2 innovations, arising between bracts and perianth, is diagnostic; rarely subfloral innovations are lacking. If there is a single innovation, this is usually soon again fertile; if there are paired innovations, these remain short and sterile. The bracts are hardly distinguishable from ordinary leaves, except in their slightly larger average size.

Sectio IV. CHOACHINAE Carl

Plants *medium sized,* usually 2.4-3.5 mm wide, with usually *distant to slightly imbricate leaves; brownish with age, shiny,* the brownish *stems rigid and flexuous, but quite fragile* (especially when dry). Branching diffuse, *intercalary, monopodial.* Leaves with a short, little acroscopically arched line of insertion ± *short decurrrent dorsally, very short-decurrent ventrally;* antical and ventral bases ± reflexed, the leaves thus antically convex; *leaves narrow basally,* either remaining narrow throughout their length (then *oblong to lingulate*), or broadening above their narrow bases (*then ovate to obovate*), *ca.* (1.2) 1.4-2.4× as long as wide, with a *distinct tendency to develop two relatively distinct apical teeth or lobes; leaf-margins spinose-dentate* (but the teeth sometimes few, except for the two apical ones), the teeth sharp and narrow- to broad-based; *teeth usually 2-12 (16) per leaf.* Leaf cells *moderate in size, becoming ± equally thick-walled, ca.* 22-28 μ apically, 22-28 x 21-35 medially, *slightly collenchymatous, the trigones not or barely bulging* (rarely strongly so); leaves with marginal cells not or equally thick-walled, not forming a discrete border; basal cells little to moderately elongate, *not forming a distinct vitta,* 1.5-2.5 × as long as wide; oil-bodies *3-7 per cell,* relatively large (to 7 x 10 μ), *of the grape-cluster type* (in our species). *Underleaves minute, of 1-several capillary uniseriate divisions* that are free nearly to base. *Reproduction usually asexual, by means of fragile, freely caducous leaves; shoots often largely denuded.*

Perianths with a dorsal wing always developed (*fide* Carl; our species not certainly known with perianths). Androecia *longly spicate, slender,* often of up to 10-12 (16) pairs of bracts; bracts 1-2-androus, strongly ventricose, except for the apices erect, the spreading to reflexed apices, and antical and postical margins, spinose-dentate (two of the distal teeth often more prominent, lobe-like); antical base commonly with a sharp tooth, which is often inflexed; bracteoles small, usually of 2-4 nearly completely discrete cilia.

The Choachinae are a heterogeneous lot, as restricted here, in which I follow Carl (1931). Carl admits that "zwei Formenkreise setzen diese Sektion zusammen. . . Bei dem ersten sind die Blätter stets ampliat, in der zweiten Gruppe gehören sie meist dem *Patulae*-Typus an." Carl does not believe these two groups can be clearly separated. The most important single feature uniting the group, it

seems to me, lies in the free formation of caducous leaves; to this should be added the sparsely spinose-dentate leaf-margins (with the teeth less than 15 per leaf), the shiny texture, and tendency towards brownish pigmentation. Our two representatives clearly have patulate leaves; this is also the case in such characteristic species as the European *P. punctata* (a species Carl also places in the Choachinae), in *P. choachina*, a neotropical species exhibiting the most immediate relationships to *P. punctata*, and in the polymorphous *P. japonica*, a species exhibiting affinities to both the Choachinae and the Subplanae.

However, even the affinities among these patulate-leaved species are obscure, as is evident from a study of the oil-bodies. In both of the nearctic taxa, *P. sullivantii* and *P. austini*, the oil-bodies are coarsely segmented, clearly of the "grape-cluster" type. In the Japanese *P. japonica* the oil-bodies are fine-segmented and nearly or quite smooth externally (see Hattori, 1951, 77, Pls. I, 27-29; III, 51; VI, 14). By contrast, the European *P. punctata* has (in the sparse living material I have seen) the oil-bodies homogeneous, occurring 4-7 per cell, at best becoming faintly barred with age! (Müller 1956, p. 898, however, states the oil-bodies are formed of spherules). The differences in cell type are also very great. In *P. sullivantii* and *austini* (coarse-segmented oil-bodies!) the cells are essentially non-collenchymatous, with the walls becoming nearly equally thickened in many cases. In *P. japonica* distinct to moderately bulging trigones occur. In the European *P. punctata* the trigones are coarse and nodular! This suggests that, perhaps, the Choachinae are not a natural group, although these species share narrow-based leaves; a tendency towards brownish pigmentation; shiny texture when dry; absence of any trace of a vitta; short-decurrent postical bases of the leaves; minute underleaves; absence of propagula, but with asexual reproduction by means of caducous leaves.

The rather problematical relationships discussed here can best be expressed in the following key to what might be regarded as subsections of the Choachinae:

1. Leaves oblong to obovate, to orbicular-obovate, rarely slightly ovate; leaf-bases without any tendency towards formation of a vitta; oil-bodies segmented or homogeneous; cuticle smooth. 2
    2. Oil-bodies segmented; cells with trigones small or moderate in size, never coarsely nodose. 3
        3. Leaves distinctly narrowed basally, rectangular to obovate; oil-bodies rather coarsely segmented; leaves dentate to spinose-dentate. Subsectio Austiniae. ....(*P. sullivantii, P. austini*)
        3. Leaves not strongly narrowed towards base, somewhat ovate to oblong; oil-bodies nearly smooth, fine-segmented; teeth of leaves aciculate. ....See Subsectio Acanthophyllae (p. 337) (*P. japonica*)
    2. Oil-bodies homogeneous (as far as known); cells with coarse, bulging trigones; leaves rotund-ovate to rotund-obovate. ....Subsectio Choachinae (*P. punctata, P. choachina*)

1. Leaves distinctly ovate, ampliate, widest slightly above base; leaf-bases with a tendency towards formation of a weak vitta (cf. *P. oxyphylla* Spr.; *P. spinulosa* (Dicks.) Dumort.); oil-bodies homogeneous (in *P. spinulosa*); cuticle often verrucose (*P. oxyphylla, P. guadalupensis*) ....Subsectio Spinulosae (*P. spinulosa, P. oxyphylla, P. acanthoda, P. guadalupensis*)

In addition to the preceding types Carl (*loc. cit.*, p. 83) also includes *P. exesa,* a species of central and northern South America, and *P. lacerifolia,* an Andean species, in the Choachinae. I have strong reservations about the wisdom of including these species with the Choachinae, which I believe are best restricted to species able to drop their leaves. *P. exesa,* as Carl (1932) has shown, as well as *P. lacerifolia,* reproduce asexually by means of caducous, modified teeth of the leaves. This suggests an affinity to the Bidentes, rather than to the Choachinae. Should these species possess homogeneous oil-bodies I would not hesitate to transfer them to the Bidentes.

The Subsectio Acanthophyllae, I believe, belongs in or at least near the next section, the Sectio Subplanae, under which it is placed on subsequent pages.

Finally, the ampliate-leaved species, with ovate leaves that are not deciduous, and with homogeneous oil-bodies, typified by *P. spinulosa,* a European species, probably should also be removed from the Choachinae. The European authors repeatedly emphasize that *P. punctata* and *P. spinulosa* are closely related; I have reservations about the correctness of this assumption. It is probable that this group of species, here placed in the Subsectio Spinulosae, should be attached to the Zonatae, to which they are allied in leaf-form, cell-type (although not in cell-size!), the homogeneous oil-bodies, the postically secund leaves, and other characters.

Since I am not convinced that the preceding three complexes can be retained in the Choachinae, I have based the diagnosis of that section entirely on the Subsectio Austiniae and Subsectio Choachinae.

From the preceding outline it is clear that, with the removal of the Acanthophyllae, the Subsectio Austiniae acquires an isolated position in the Choachinae. It differs from the other Choachinae that have been cytologically investigated (*P. punctata, P. spinulosa*) in the coarsely segmented oil-bodies. In addition to this, the species are distinguished by the slight ability to develop collenchyma, sharply bulging trigones apparently never being developed, although the cell-walls tend to develop equal layers of thickening, with ill-defined localized, intermediate thickenings and trigones. It is quite possible that the Austiniae should be removed from the Choachinae. They fail to fit more clearly into any of the other sections established by Carl. Consequently, further study may demonstrate the desirability for elevating the Austiniae to the rank of a full section.

Our two species stand isolated among other nearctic Plagiochilae. They exhibit some affinities with the Sectio Bidentes, emphasized by the frequent marked indication of bilobing of the leaves (*P. austini*), by the mode of asexual reproduction, the brownish pigmentation, the fragility of the plants, and their shining cuticle. However, the segmented oil-bodies, the inability to develop sharply defined and bulging trigones, and the larger size serve to adequately separate the two regional members of the Choachinae from any of the Bidentes. In these three respects, our members of the Choachinae approach *P. japonica* (Subsectio Acanthophyllae), a species exhibiting affinities to both Choachinae and Subplanae. This relationship is emphasized by

the ability of *P. sullivantii* to produce sharply spinose marginal teeth of the leaves, recalling the aciculate teeth of *P. japonica,* and of the Subplanae as a whole.

The apparent transition between our species of the Choachinae and the Subplanae, as indicated by a study of *P. sullivantii, P. japonica* and their allies, is disturbing. The Choachinae, in apparently all cases, freely develop caducous leaves; they generally lack the long and slenderly aciculate marginal teeth of the leaves that characterize the Subplanae. Furthermore, they generally have leaves that, in drying, do not remain flat, but become variously convolute, and/or postically secund. Furthermore, their cells usually average smaller in size. The Subplanae typically lack caducous leaves (but see also p. 349); possess aciculate, elongated marginal teeth of the leaves; have leaves that are virtually flat both when moist and when dry, and have unusually large and pellucid cells. To these distinctions may be added the putative difference in oil-bodies, those of the Choachinae being homogeneous or divided into coarse and protuberant segments ("grape-cluster type"), while those of the Subplanae are mostly granulose and fine-segmented. Study of longer series of species may break down any such distinction. On the other hand, study of fertile material, not available of most species, may demonstrate the existence of major differential characters not at present known.

At one time (Sullivant, 1845), our two species of Choachinae (*i.e., P. sullivantii* and *P. austini*) were considered to be identical with the European *P. spinulosa* (which, at that time, also included the European *P. punctata*). *P. punctata* is a typical member of the Choachinae, being extremely close to the neotropical *P. choachina. P. spinulosa,* as we have seen, occupies a somewhat isolated position in the Choachinae, together with a series of allied Neotropical species (*P. oxyphylla* Spr., *P. acanthoda* Spr., *P. guadalupensis* Spr.). In these species the leaves tend to be ovate and ampliate, with a broad insertion and relatively long antical decurrence, and the base of the leaf is obscurely vittate. In these respects the species exhibit an affinity with the Sectios Arrectae, Zonatae and Renitentes (none of which, however, include species developing caducous leaves). Whatever the affinity of these two European Choachinae, they are only distantly allied to our two regional species, possessing coarse trigones and homogeneous oil-bodies.

Branching in the two regional species of the Choachinae is closely similar to that in the Zonatae and the Asplenioides; *i.e.,* it possesses (*i.e.,* in *P. austini*) the following characteristics: a leafy axis producing three types of branches (*a*) intercalary leafy branches from the upper portions of the shoots; these are always positively phototropic, and never give rise to stolons; (*b*) intercalary leafy branches from the older portions of the shoot; these originally diverge at nearly right angles, but become abruptly strongly ascending; these branches give rise, usually at some distance from their origin, to negatively phototropic rhizoidous stolons; (*c*) intercalary branches from the older shoot sectors that are negatively phototropic from the time of their origin and fail to develop normal leaves; these form stolons. The branches of type *b* closely approach those of the genera *Chiastacaulon* and *Plagiochilion* (*Noguchia*); they differ in that the stoloniferous branches originate in leaf axils, hence laterally rather than postically. As far as known, all the leafy branches are also clearly intercalary in origin, hence furcate branching fails to occur.

PLAGIOCHILA SULLIVANTII G. ex EVS.

Figs. 24-26; 27:7-8

Plagiochila spinulosa Sullivant, Musci Alleghaniensis No. 219 (*nec* Dumortier, Rec. d'Obs. 15 (1835) = *Jungermannia spinulosa* Dicks., Fasc. Crypt. 2:14 (1801).

Plagiochila sullivantii Gottsche ex Evans, Bot. Gaz. 21:191, 1896 (as to type; in part only).

Plagiochila alleghenienis Evans ex Stephani, Bull. Herb. Boissier, Ser. 2, 3:334 (1903); also Spec. Hep. 2:318 (1903).

Plagiochila sullivantii Evans, Rhodora 16:68 (1914); The Bryologist 18:82, 1915 (in part only).

Plants showing differentiation into prostrate leafless caudex and (usually diffuse) erect to suberect, slender, simple or subsimple, leafy, aerial shoots, deep green, becoming brownish with age, *rather glossy.* Leafy shoots *ca.* 1.4-1.8, occasionally 2.2-3.2 mm wide, 5-12 (18) mm long; branches rare or absent, when present monopodial. Stem brownish, stiff and rigid, somewhat flexuous, usually standing at right angles to the substrate or ascending, 180-240 μ in diameter; cortex brownish, dorsally of cells 16.5-18 μ wide x 35-65 (85) μ long, ventrally similarly wide but 45-75 (85) μ long. Leaves quite *distant to approximate,* rarely slightly imbricate, spreading in a flat plane horizontally, at an angle of (45-50) 55-75° with stem; leaves *ca.* 650-690 μ wide x 900-1050 μ long (exclusive of apical teeth; with teeth *ca.* 1100-1200 μ long) to (680) 720-900 (1100) μ wide x 1200-1350 (1450) μ long (*length usually 1.25-1.6 × the width*); line of insertion *ca.* 600-650 (850) μ long; leaf shape *essentially obovate to rectangular-obovate on mature leaves,* occasionally rectangular-ellipsoid, *widest at or* (*more usually*) *above middle;* dorsal margin slightly reflexed on basal one-third to one-half, forming a rather obscure cnemis; postical base with margin often narrowly reflexed; *leaf scarcely decurrent ventrally, short-decurrent dorsally,* usually rather obviously narrowed to the relatively short line of insertion. Leaf-margins usually with 5-10 (occasionally 10-15) *spinose, narrow-based, sharp teeth,* some of which end in a *uniseriate row of* 2-3, *occasionally* 4-5 *elongate cells* (cells to 33-38 (48) μ long x 14-17 μ wide); the two apical teeth often coarser and representing the putative primary lobes of the leaf, but *most often the apical teeth scarcely or not coarser, the leaf thus with only a weak tendency to show the atavistic bilobing;* postical margin usually with 2-5, occasionally 7, teeth below apex extending to within 1/5 of base; antical margin with 0-2 teeth near apex, otherwise edentate; antical margin straight to very slightly arched, postical, weakly to moderately, but more strongly arched. Cells polygonal near leaf-middle, 22-26 (28) μ wide x 24-30 (35) μ long; near margin just below apex (16-18) 22-25 μ wide x 21-25 (30) μ long; cell-walls thin to *more or less evenly thick-walled, with small or minute* (*never*

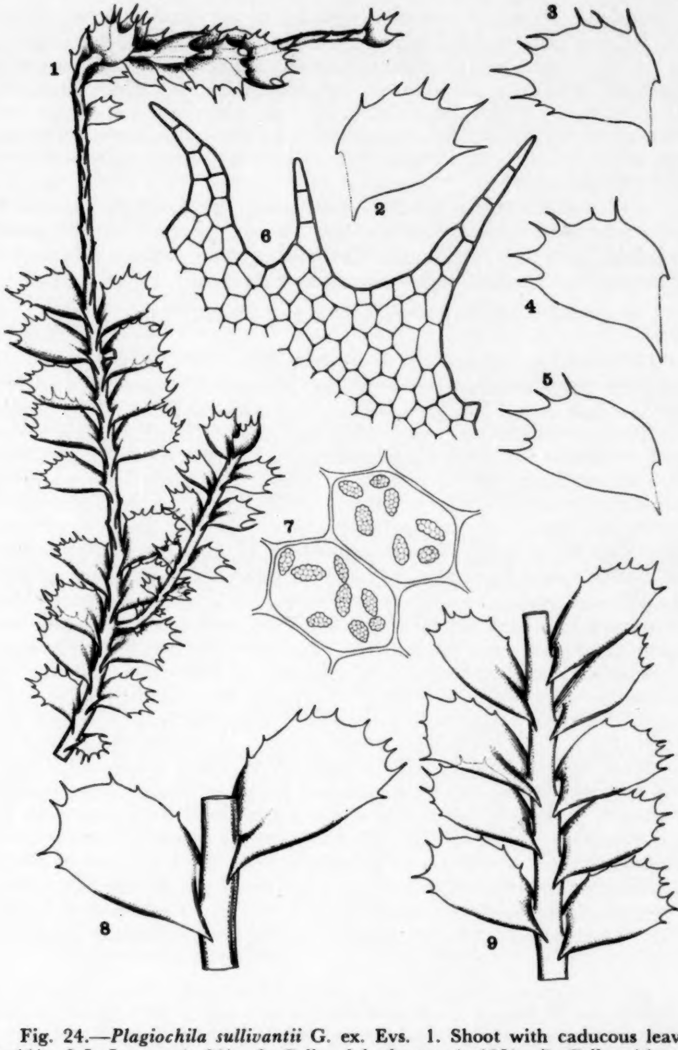

Fig. 24.—*Plagiochila sullivantii* G. ex. Evs. 1. Shoot with caducous leaves (x 11); 2-5. Leaves (x 21); 6. Cells of leaf-apex (x 185); 7. Cells with oil-bodies (x 540); 8. Shoot-sector, with leaves *in situ* (x 27); 9. Same (x 22). (Figs. 1-5 from type specimen; 6, 8-9, from *Sharp* 38103.)

distinctly bulging) *trigones;* oil-bodies more or less fusiform to broad-ellipsoidal, *formed of relatively few coarse, protruding globules* (thus segmented, grading to coarsely papillose, of the "grape-cluster" type), (3) 4-7 per cell, *ca.* 4.8-5 x 6 to 5 x 8-9 μ; chloroplasts dense, copious, *ca.* 4 μ. *Underleaves minute,* usually consisting of 2-4 uniseriate capillary filaments terminated by slime-papillae, rarely 1-seriate. *Asexual reproduction by caducous leaves,* some mature shoots with long areas quite denuded, the leaves of caducous regions sometimes somewhat reduced, as wide as long, and more strongly spinose-dentate than normal leaves.

Male plants rare; bracts 1-2-androus, erect except at apices, spinose-dentate. Female plants with bracts suberect, rather closely sheathing perianth at base. "Perianth ovoid-cylindric, about 1/2 emergent; mouth dentate." [3] Sporophyte unknown.

Type.—Virginia, without definite locality, *Sullivant.*

Distribution.—Apparently a relict of the old Tertiary forest of the Southern Appalachians, but extending altitudinally upward well into the Spruce-Fraser Fir-*Rhododendron catawbiense* Zone. The species is almost never found below 2500 ft. altitude, and extends up to 6684 ft. in the Southern Appalachians; it appears restricted to above 3600 ft. at the northern end of its range. The species very rarely penetrates to an elevation as low as 1800-2000 ft. in the Escarpment Gorges of the Southern Appalachians (as in the Whitewater and Chattooga R. ravines). In this respect the plant is more tolerant than the closely allied *P. austini,* which appears unable to survive at such low altitudes, at least southward. Evans (1915) explicitly stated that the species had been known from only two collections (Virginia and North Carolina), and extended its range to Georgia (but this report is erroneous for *P. caduciloba*). Almost all subsequent reports, on verification of material, prove to represent the errors in determination. The species has been erroneously reported from Georgia (by Evans, 1915, p. 82; Ammons, 1940; Jacobs, 1954) and from Florida (by Kurz and Little, 1933; Frye and Clark, 1944; Redfearn, 1952). The Ammons report from Georgia was based on material determined by Evans in the NYBG; this I have examined and found to be *P. caduciloba* (Fig. 27:1-2, 7, 9); the Jacobs report is merely compilation from the literature. The reports from the Piedmont of North Carolina (Durham, Stokes and Orange Cos.) in Blomquist (1936) represent errors in determination for *P. yokogurensis* subsp. *fragilifolia.* The Ammons (1940) report from New Hampshire is evidently

[3] The description of the perianth is based on Gottsche's manuscript notes, as is brought out in the discussion of Evans (1896, p. 192). Evans states he has seen no perianth-bearing material, and no female plants could be found in the copious personal collections I have made, or in any herbarium material studied. Therefore, it must be regarded as very possible that the female plants Gottsche attributed to *P. sullivantii* do not belong here.

an error for *P. austini;* her report from Florida is evidently based on that of Kurz and Little (1933). The latter figure a plant with leaves fully twice as long as wide which probably represents a divergent-leaved *P. floridana* or perhaps *P. dubia,* though their drawing is not accurate enough to make identification certain; this drawing is unfortunately reprinted in Frye and Clark (1944: Fig. 3, p. 440). Among their "Examinations" Frye and Clark list the species from Key Largo and Timms Hammock, in Monroe and Dade Counties, respectively, from the tropical part of Florida. These determinations are surely incorrect, as is a collection listed by them from Pensacola, Florida (*Frye*). The lack of comprehension of this species is emphasized by the statement (*loc. cit.,* p. 440) in which these authors express their doubts as to whether the species is distinct from *P. virginica,* a totally unrelated taxon. The Redfearn reports from Florida appear again to be mere compilations of the erroneous literature. Adding to the chaos, we find that Frye and Clark figure a plant of *P. austini* (their fig. 1) as *P. sullivantii.* Of the three illustrations given by them, only their fig. 2, taken from the Evans (1896) paper represents true *P. sullivantii.*

The report of the species from Overton Co., Tennessee (Clebsch, 1954) is based on *P. asplenioides.* The material reported from Blount Co. Tennessee (Sharp, 1939) is *P. echinata,* as is some of the material from Sevier Co. in the Tennessee Herbarium.

VIRGINIA: Without definite locality (Sullivant, Musci Allegh. Exsic. No. 219, 1843, *type!*); near summit White Top Mt., *ca.* 5400 ft., Smyth Co. (*Schuster* 38083, 38083a, with *Metzgeria hamata*). WEST VIRGINIA: Monongalia and Pocahontas Cos. (Ammons, 1940). NORTH CAROLINA: Andrews Bald, near Clingmans Dome, Smoky Mts. (*Taylor,* 1929; *Schuster* 40187); Linville Gorge, Burke Co., below falls (*Schuster* 29013!); same data, 1-2 mi. below falls (*Schuster* 29076); near Highlands, Cullasaja Gorge, Macon Co. (*M. S. Taylor* 2423); Dry Falls NW. of Highlands, Macon Co. (*Schuster* 36504; 25241, *p. p.,* among *P. austini; Schuster* 25264a, *p. p.,* among *Metzgeria hamata; Schuster* 25237, *p. p.,* among *Radula sullivantii; Schuster* 25256, *p.p.,* among *Plagiochila caduciloba*); Green Knob, Balsam Mts., 5150 ft., SE. of Sunburst, Haywood Co. (*Anderson* 11271!); recessed cliff-face, Roan High Bluff, Roan Mt., Mitchell Co., *ca.* 6100 ft. (*Schuster* 38651); Andrews Bald, SW. of Clingmans Dome, Swain Co. (*Schuster* 39756, 39757, *p. p.,* with *P. tridenticulata*); branch from Fork Ridge just above jct. with W. Fork Pigeon R., S. of Sunburst, 4500-4600 ft., Haywood Co. (*Schuster and V. Bryan* 39482); Richland Balsam, E. of summit, 6200-6300 ft., Haywood Co. (*Schuster* 39789, 39799); beneath and in spray of High Falls, Whitewater R., Jackson Co. (*Schuster* 40664; with *Metzgeria hamata, Selaginella apoda*); Robinson Creek near jct. with Slattern Branch, 3200 ft., Jackson Co. (*Anderson* 10501, *p.p.,* with *Plagiochila austini;* plate); near summit of Grandfather Mt., 5800 ft., Caldwell Co. (*Schuster* 30183b, 30180a, *p.p.,* with *Eremonotus minutus, Scapania nemorosa, Bazzania denudata, Herberta sakuraii*); Lower Rock Bridge, above Bonas Defeat, E. fork of Tuckasegee R. at 3000 ft. (*Anderson* 10614!, 10633! *p.p.,* with *P. austini* var. *stenophylla*); Spruce-Fir Zone, Mt. Mitchell, 6684 ft., Yancey Co. (*Anderson and Jones* 9743!); below Windy Falls, Horsepasture R., Transylvania Co., 2000 ft. (*Anderson* 8472!); below

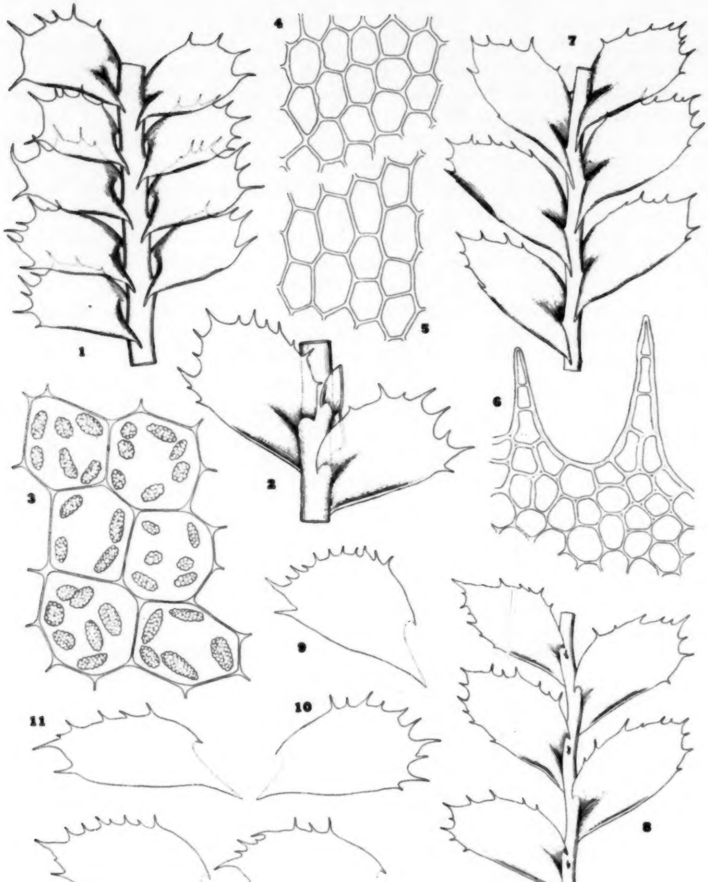

Fig. 25.—*Plagiochila sullivantii* G. ex Evs. 1. Sector of small shoot with relatively broad leaves (x 20); 2. Same, postical aspect (x 23); 3. Median cells of mod. *leptoderma* (x 525); 4-5. Median and basal leaf-cells, respectively, showing equally thickened walls (x 175); 6. Apical cells showing dentition (x 180); 7-8. Antical and postical aspects of plants of mod. *angustifolia,* approaching var. *spinigera* (x 12.5); 9-13. Leaves, showing range of variation (x 16). (Figs. 1-2, from *Sharp* 38103, Tenn.; 3. Grandfather Mt., N.C., *Schuster;* 4-13, Linville Gorge, N.C., *Schuster* 28916, in part trans ad var. *spinigera.*)

Rainbow Falls, Horsepasture R., *ca.* 2520 ft., S. of Oakland, Transylvania Co. (*Schuster and Anderson* 34726); Linville Gorge, 1-1.5 mi. below Falls, on shaded, moist rock face, Burke Co. (*Schuster and Jones* 28916; type of the var. *spinigera,* which see below); Whitewater R. gorge, *ca.* 1/8 mi. below High Falls, Jackson Co. (*Schuster* 34737, with *P. caduciloba, P. virginica caroliniana*); Cullasaja Falls, NW. of Highlands, Macon Co. (*Taylor* 2204!). TENNESSEE: Pinnacle Mt. Trail, Sevier Co., 3800 ft. (*Sharp* 341092!); Greenbrier, Smoky Mts., Sevier Co., 2500 ft. (*Clebsch and Redfearn,* 1949!); Birch bark, Grassy Patch, Smoky Mts., Sevier Co., 4700 ft. (*Sharp* 38103!); Mt. Le Conte, Sevier Co., 4000 ft. (*Sharp* 35166!); above Alum Cave parking lot, Sevier Co., 4000 ft. (*Sharp* 5164!); along small branch of West Fork of Little Pigeon R., above Chimneys Parking area, *ca.* 4500 ft., Sevier Co. (*Schuster* 36516, 36530, 36514); Mt. Guyot, Smoky Mts., Cocke Co., 4000 ft. (*Sharp* 109!, 1930; mod. *parvifolia,* with freely caducous leaves). GEORGIA: Chattooga River, W. side below Ellicott Rock, barely but definitely within the NE. corner of Rabun Co., 2000 ft. (*Schuster and V. Bryan* 39831d, *p. p.;* only a few plants, but these with caducous leaves and coarsely segmented oil-bodies, hence definitely referable to *P. sullivantii;* associated with *Lophocolea muricata, Radula obconica, Harpalejeunea ovata, Plagiochila asplenioides, P. sharpii* and *P. caduciloba;* the southernmost station of the species). SOUTH CAROLINA: Whitewater R. Gorge, Oconee Co., just above the Middle Falls, on W. side of gorge, just below the N.C. border (*Schuster* 40553). Plants from Mississippi (Harrison Co., *Webster and Wilbur* 756) which have been widely distributed in herbaria as *P. sullivantii* (det. H. Crum) represent a form of *P. floridana* approaching *P. dubia.*

Ecology.—The present species is almost identical in its habitat "requirements" with the closely related *P. austini*—both species are restricted largely to shaded (often densely shaded and overhung) rock-walls and ledges, often around water falls, where there is a very high, constant, atmospheric humidity—but where the plants are protected from rain. The two species frequently are admixed (as in *Anderson* 10501, 10633; *Schuster* 25241, etc.). Typical occurrences are (1) on the underside of a strongly projecting ledge (near summit of Grandfather Mountain, North Carolina, *Schuster* 34108a), there with *Eremonotus minutus, Scapania nemorosa, Plagiochila asplenioides,* and *Herberta sakuraii;* where the light intensity was highest, the writer was unable to obtain any light reading (reflected light) from this habitat; (2) on strongly, constantly shaded, partly overhung ledges beneath and near the sides of Dry Falls, N. C. (*Schuster,* 25241, etc.), where the plants occurred with *Plagiochila austini, P. caduciloba, Herberta sakuraii, Bazzania denudata* and *tricrenata,* etc.; the plants occurred just within to just outside of the spray-zone of the waterfall. (3) On densely shaded rock-wall, in deep recess, Linville Gorge, below Falls (*Schuster and Jones* 28916), associated with *Metzgeria hamata, Riccardia multifida, Jubula pennsylvanica,* and the moss *Hookeria acutifolia.*

Very rarely the plant occurs on birch bark in the mountains, at high elevations (4700 ft. as in *Sharp* 38103). The plants here are much reduced, occurring as a xeromorphic phase with very freely

caducous and reduced leaves, often approaching *P. tridenticulata* in size and facies. Such plants are associated with *Radula tenax* and *obconica, Lejeunea lamacerina gemminata, Harpalejeunea ovata* and *Metzgeria.*

Differentiation.—*P. sullivantii* is a relatively rare and localized species which has had, nevertheless, a relatively complicated nomenclatorial history, and has been confused with a wide range of species. Indeed, less than 40 percent of the material cited as this species, in the literature, and of the collections examined in herbaria, belongs to *P. sullivantii;* much of it is referable to *P. echinata.* In spite of this, *P. sullivantii* is perhaps one of the most distinctive and easily recognizable species of the genus.

Normal, well-developed shoots differ from all of our other Plagiochilae in the fundamentally obovate or obovate-oblong leaves, perceptibly narrowed in their basal halves. None of our other Plagiochilae possess unlobed leaves that are widest at or beyond the middle. The species is clearly allied only with *P. austini,* as is evident from the fact that Evans, an astute worker, for some years (1896-1914) included the latter under *P. sullivantii.* However, the repeated association of the two species, and their decidedly different appearance when growing under identical conditions (compare Fig. 27:5-6 and 27:7-8) preclude the possibility of their representing a single species. At one time it was believed that they might represent the two sexes of a single species, the differences being assignable to secondary sexual distinctions. However, in Fig. 27:5-8 are illustrated male plants of the two species, demonstrating the fallacy of such a hypothesis. Furthermore, the two species "behave" differently under identical conditions. In the plants of *Anderson* 10501 (from which the indicated figures are drawn) *P. sullivantii* freely produces caducous leaves, the *P. austini* is apparently uniformly persistent-leaved. This suggests that the stimuli leading to leaf-dropping in one species are not the same (at least quantitatively) as those leading to formation of caducous leaves in the other. Clearly, physiological differences also serve to separate these two taxa.

The morphological differences separating *P. sullivantii* from *P. austini* are largely derived from the leaves and the leaf-cells. The leaf shape usually easily separates *P. sullivantii* from the narrower-leaved *P. austini.* Furthermore, juvenile leaves of *P. sullivantii* rarely are sharply bilobed or bidentate—a character very usually present on small leaves of *P. austini.* The prevailing, basic, bilobed nature of the leaves of *P. austini* is readily evident from Figures 28 and 29. This *is especially marked,* on the younger leaves of branches, and the leaves are there bilobed 1/3-3/5, with the lobes entire and acuminate, or rarely with 1 or 2 lateral teeth on submature leaves (Fig. 28:2-3, 7, 11). Compare this to the condition in *P. sullivantii,* where (see Fig. 26:3; of the type, Fig. 24:1) both immature leaves of main shoots and the young leaves of branches are predominantly obovate, and bear 4-6 or more spinous teeth even on small leaves: these teeth are

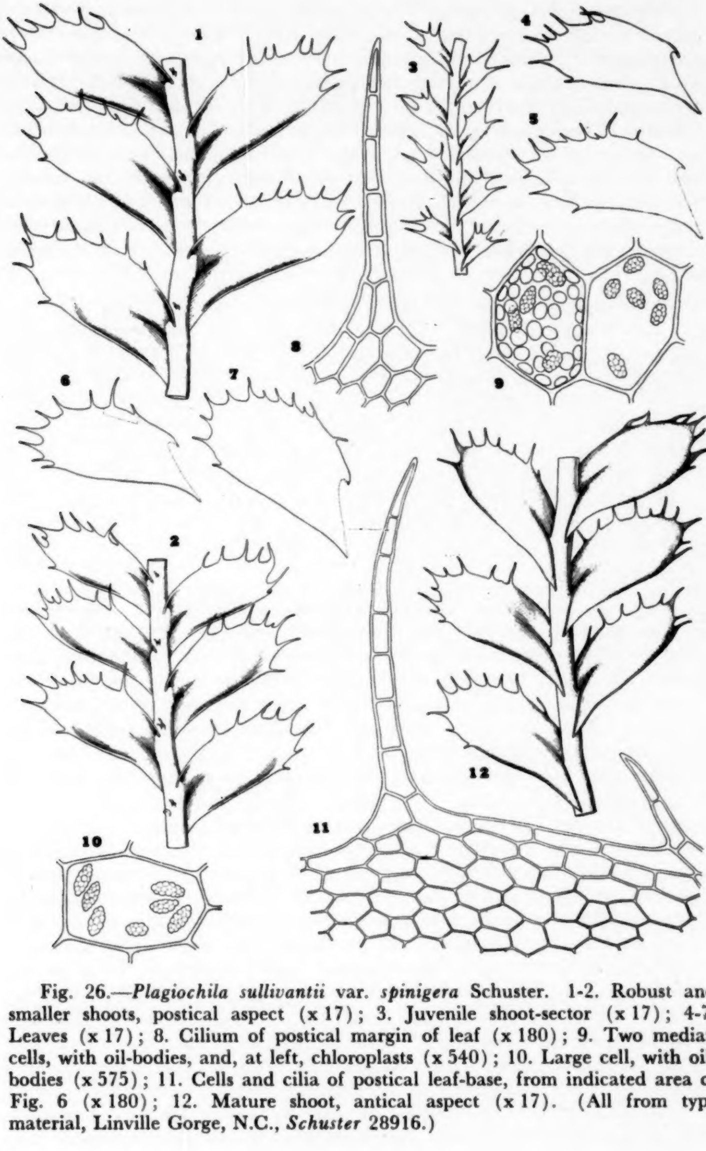

Fig. 26.—*Plagiochila sullivantii* var. *spinigera* Schuster. 1-2. Robust and smaller shoots, postical aspect (x 17); 3. Juvenile shoot-sector (x 17); 4-7. Leaves (x 17); 8. Cilium of postical margin of leaf (x 180); 9. Two median cells, with oil-bodies, and, at left, chloroplasts (x 540); 10. Large cell, with oil-bodies (x 575); 11. Cells and cilia of postical leaf-base, from indicated area of Fig. 6 (x 180); 12. Mature shoot, antical aspect (x 17). (All from type material, Linville Gorge, N.C., *Schuster* 28916.)

usually subequal in size. Furthermore, in **P.** *sullivantii* immature leaves are often quite broad and only 1.1-1.4 × as long as wide; by contrast, in **P.** *austini,* the juvenile leaves and leaves of slender shoots tend to be strongly elongate, parallel-sided, 1.9-2.3 × as long as wide (compare Fig. 25:1 and Figs. 29:1, 30:2). Thus, the differential features of these two species are *as strongly marked on juvenile shoots and leaves as on mature ones.* However, even on the most robust shoots of **P.** *sullivantii,* we find that the two largest teeth (or "lobes") are scarcely marked, while on the most robust shoots of **P.** *austini* there is a discrete retention of two main lobe-like teeth, each usually supplied on each margin with 1-3 supplementary spinose teeth much inferior in size.

Both species agree in the fragile leaves, which show a strong tendency to be caducous. Caducous leaves have not been previously noted in **P.** *sullivantii,* but are present in *Sharp* 38103 (Tennessee. Sevier Co.: Grassy Patch, on birch bark at 4700 ft.) and *Schuster* 28916 (Linville Gorge, N. C.), as well as in most other specimens of the species examined. I have carefully studied the type specimen, **P.** *spinulosa* Sull. Musci Alleg. No. 219 (not [Dicks.] Dumort.). This, as Evans (1914) has shown, is quite different from **P.** *sullivantii, sensu* Stephani (who used the name *sullivantii* for the plant we now know as **P.** *austini*). At least that portion of the type of **P.** *sullivantii* in the New York Botanical Garden consists of plants with quite strongly caducous leaves.

The type material is also characterized by the strong development of the spinous, aciculate marginal teeth (which are often 8-9 cells long and then 5-6 cells wide at base, terminated by 3, less often 2 or 4 elongate, superimposed, single cells, which average 32-36, sometimes 40-43 μ long). In the type the marginal distal cells are mostly 16-18 x 25 μ (less than 1.7 × as long as wide); the median cells are virtually isodiametric, 23-25 μ wide x 25-28 μ long; the basal cells are only little elongate and little larger than the median cells (24-27 μ wide x 30-35 μ long). It should also be noted that the obovate form of the leaf is most marked when plants are examined without too much pressure, for then the basal half of the postical margin is usually quite decurved, thus appearing to narrow the postical base of the leaf, and giving the leaf the typical obovate shape. When the leaves are flattened out, they are often only slightly obovate (Fig. 24: 2, 5) or may, exceptionally, approach slightly ovate (Fig. 24:3-4). It is thus apparent that the relatively broad leaves, as much as the leaf-shape and the much more slender and acuminate, more narrow-based teeth of the leaves (and their usually more luxuriant development) serve best to separate **P.** *sullivantii* from **P.** *austini.* In extreme forms of **P.** *sullivantii* (such as *Schuster* 28916) the leaf-shape becomes extremely narrow, with the leaves often averaging 650 μ wide x 1300 μ long, *i.e.,* fully twice as long as wide. In such cases the leaf is narrowly rectangulate, but slightly wider distally than near base

(retaining a suggestion of the obovate shape). The basic dimensions of the leaf then approach those of *P. austini,* and one must rely on the narrow spinous nature of the dentition and the form of the leaf-cells to affect a separation between the two species.

In some cases, the leaf-cells also offer what appear to be points of distinction. In *P. sullivantii* the marginal cells at and above the leaf-middle are usually little elongate (parallel to the margin), and merely 17-20 μ wide x 26-30 (rarely 32-34) μ long; the cells of the leaf-middle are nearly isodiametric and 20-25 μ wide x 23-28 μ long; the cell-walls are everywhere relatively thin, and the trigones are minute or small; the longitudinal walls of the leaf-cells are not irregularly thickened in the median and basal leaf-cells. By contrast, in *P. austini,* the marginal cells are usually strongly elongate, and vary from 25-34 μ long x 13-15 μ wide to 44 μ long x 17 μ wide (*i.e.,* they average 2-2.5 × as long as wide); the cells above the leaf-middle may be nearly isodiametric (20-22 x 25-30 μ), but at the leaf-middle and below they become more or less strongly elongate and 20-23 μ wide x 32-36 μ long; the longitudinal walls are often thickened.

These differences in cell-dimensions are basically due to the shorter leaf-form of *P. sullivantii* (as contrasted to the narrowly rectangulate leaf-form of *P. austini*). In the rare forms of *P. sullivantii* with distant, narrow leaves, the cells become correspondingly elongated. For instance, in the narrow-leaved variety *spinigera* (*Schuster* 28916, Linville Gorge, N. C.) the marginal cells at the middle of the postical margin (between teeth) are extremely elongated tangentially, often 17-20 μ wide x 36-46 μ, occasionally 52-58 μ long, and 2-2.5, rarely 3-4 × as long as wide (Fig. 26:11); such leaves, however, have little elongated median cells, 22-25 (27) μ wide x 27-32 μ long (Fig. 26:9). It is thus evident, that the elongation of the leaf-cells is partly dependent on leaf-shape. Since the leaf-shape of *P. sullivantii* may, exceptionally, be quite narrow, it further follows that the cell proportions are subject to major variation. Therefore the distinctions drawn between the two species, in this regard, appear to be almost bridged over.

The marginal teeth of *P. sullivantii* are also narrow-based, with the coarser teeth only 3-6 cells wide and not evidently lobe-like, whereas in *P. austini* the larger distal teeth are often lobe-like and 6-10, occasionally 11-12 cells wide at base. In the final analysis, the narrow teeth of *P. sullivantii* constitute the most important sole characteristic serving to separate it from the related *P. austini.*

In addition to the real relationships of the species with *P. austini,* there has been unnecessary confusion of the species with at least four other nearctic species; *P. virginica, P. floridana, P. echinata* and *P. caduciloba.* Frye and Clark (*loc. cit.*) state that the only described differences between *P. sullivantii* and *virginica* to "which one could attach much significance" lie in the supposed presence (*sullivantii*) or absence (*virginica*) of the underleaves. As is developed under *P. virginica,* this distinction affords no separation whatsoever, since the *P. virginica* also has underleaves while juvenile shoots of *sullivantii*

may also virtually lack them. The ovate leaf-form of *virginica* and persistent leaves are two, among many, important characters that at once separate it from *P. sullivantii.*

Material of *P. floridana* has also been confused with *P. sullivantii.* However, the dull, green to olive-green color of the leaves of the former, the persistent leaves that may develop brood-bodies, and the narrower leaves that show a slight tendency to be ovate-rectangular—i.e., dilated near the postical base—will at once separate *P. floridana* from *P. sullivantii.*

Finally, it has been mentioned that previously published Georgia reports of *P. sullivantii* appear to be based on confusion with *P. caduciloba.* The fragmenting, fragile leaves, whose bases are, however, clearly persistent, the smaller size, the homogeneous oil-bodies, and the very different form of the marginal teeth of the leaves, all clearly separate *P. caduciloba* from *sullivantii.* Again, there is no close relationship between the two species.

The distinction between *P. sullivantii* and *P. echinata* are treated under the latter. Among extraterritorial species, *P. sullivantii* appears to be related perhaps most closely with various species of the Sectio Choachinae. It is related to *P. punctata* Tayl., an oceanic species of England and Ireland, and shares with this the frequently obovate leaf (though this is often obovate-orbicular in *P. punctata,* and usually much shorter than in *P. sullivantii*); the much smaller trigones separate the species from *P. punctata.* Both species, as well as the other species of the Choachinae, show a well-developed tendency toward production of caducous leaves (in which they, in turn, approach the Sectio Bidentes).

P. punctata is by no means uniformly caducous-leaved. However, in *P. sullivantii* a few caducous leaves are typically usually present. In a single, quite typical collection of *P. sullivantii* (Greenbrier, Sevier Co., Tenn., 2700 ft., *Sharp* 3870, *DU*), caducous leaves appear to be absent. The plants of this collection, however, show the relatively short leaf-form of *P. sullivantii,* and possess the aciculate few marginal teeth (usually terminated by 3-5 elongate, narrow cells) typical of the species. Thus, the development of caducous leaves may be inhibited by certain environmental conditions, stimulated by others. Consequently, it is the *ability* to produce, rather than presence of, caducous leaves, that characterizes this species.

I have also studied living *P. spinulosa,* from Scotland (through the courtesy of E. W. Jones). *P. spinulosa* differs from *P. sullivantii* in a number of characteristics, among them (1) dorsally more decurrent leaves; (2) cells with bulging, usually strongly developed trigones; (3) leaves mostly ovate in shape when mature. *P. spinulosa* is clearly caducous-leaved under some conditions; presumably the expressions "sometimes flagelliferous" (in Macvicar, 1926) refers to this tendency. Perhaps the most significant feature separating *P. spinulosa* from *P. sullivantii* (and the related *P. austini*) lies in the homogeneous oil-bodies of *P. spinulosa.*

P. sullivantii appears to be at least remotely allied to the Sikkim-Himalayan *P. acicularis* Herzog (1951, p. 40, fig. 24). It shares with that species a red-brown stem, greenish leaves (when growing in shade), leaves spreading at an angle of 50-60°, occasionally 60-70°, the obovate to obovate-oblingulate leaf-shape with the base subcuneate, and the aciculate teeth of the leaves. *P. acicularis* is particularly close to *P. sullivantii* var. *spinigera* (compare Fig. 26: 4-8 with Herzog's fig. 24: b-d). *P. acicularis,* however, differs notably in its ability to develop large trigones, those of the basal cells being "trabeculato-elongatis." The similarities are possibly largely superficial.

Variation.—*P. sullivantii* is a species of restricted, nearly uniform habitats; consequently it generally shows only a relatively narrow range of variation. The plants are deep green, generally becoming brownish with age; they almost uniformly belong to the mod. *leptoderma* or *mesoderma;* always belong to the mod. *denticulata.*

However, an evident range in degree of development of the spinose teeth of the leaves occurs which is not obviously correlated with environmental differences. For instance, the type collection of the species (Sullivant, 1845) has the spinose teeth developed to the maximal degree and these may be even longer and sharper than is indicated in the description. The spinose marginal teeth of the leaves are developed even to a more extreme degree in material of *Schuster* 28916 (Linville Gorge, N. C.: a narrow-leaved form, superficially approaching *P. japonica ciliigera*). In these plants the teeth are not only longer and more aciculate, but more numerous (often 10-15 per leaf) than in "typical" forms of the species (Fig. 25:6-13). The teeth on the postical margin may extend to within a short distance of the postical base, number 4-5 or even 7-8 along the postical margin; they are often 120-180 μ or even 250 μ and 4-7 cells long (either in a uniseriate row to base, or at most 2 cells wide at base); their component cells are as much as 50 μ long x 19-24 μ wide! The larger (apical) teeth are up to 7-9 cells long x 3-4 cells wide at base. Conversely Sharp's material (*Sharp* 38103) shows less luxurious development of the marginal teeth, even though these retain their spinose, narrow-based characteristics (Fig. 24: 8-9).

The leaf-shape of this species is given as obovate, and both Evans (1914) and Sharp (1939) emphasize this as a significant differential feature from *P. austini.* However, the leaves may be short-oblong or exceptionally, even slightly ovate (Fig. 24: 2-5), and therefore considerably more variation in leaf-shape must be admitted for the species than is usually given. This variation occurs within the population. The leaves, *in situ,* however, have the basal one-fourth or so of both antical and postical margins somewhat reflexed, thus resulting in a much more distinctly obovate appearance than when the dissected leaf is flattened out. This is not the case in *P. austini,* where the leaves retain their parallel-sided form *in situ,* or when flattened. The much more strongly arched posterior leaf-margin of *P. sullivantii* sets the species off, under all conditions, from *P. austini,* where postical and antical leaf-margins are characteristically almost straight, and almost parallel-sided for much of their length.

Studies of a series of specimens suggests that the phase of the species with unusually elongated, sharply spinose-margined leaves cannot be "explained" away as an environmental modification. It is therefore separated as a discrete variety.

Plagiochila sullivantii var. **spinigera** var. n.

Fig. 26

P. sullivantii similis; differt: foliis augustius rectangulatis, vix obovatis, *ca.* 2-2.6:1, marginibus 9-15 dentibus linearibus, aciculatis

ad 5-7 cellulas longis praeditis. Typus: Linville Gorge, Burke Co., North Carolina (*Schuster and Jones* 28916).

Similar to *P. sullivantii*, but differing as follows: (1) leaves narrowly rectangular, with a mere suggestion of the obovate shape, when flattened with anterior margin straight, posterior margin very slightly curved usually, the leaf almost parallel-sided but slightly broadened from base to above the middle: leaf dimensions, on mature shoots with length to width *ca.* 2:1, varying from 650 μ wide x 1300-1400 μ long (exclusive of teeth) to 1000 μ wide x 1950 μ long, averaging fully twice as long as wide; (2) leaves very copiously dentate, with mostly 9-15 teeth per leaf, usually 6-9 along the postical margin (of which one usually occurs near the base); (3) teeth exceptionally aciculate, on robust shoots 5-7 cells long on the postical margin, and only 1-2 cells wide at base (the length often *ca.* 200-250 (280) μ; the cells *ca.* 36-50 μ, occasionally 60-70 μ long and 2.5-4 × as long as wide); the teeth at the leaf apex often 3-4 cells wide x 5-8 cells long; (4) marginal cells equally thick-walled, those at middle of posterior margin (between teeth) strongly elongate, varying from (16) 17-20 μ wide x 36-46 μ long to, exceptionally, 15-17 μ wide x 52-58 (60-80) μ long (2-3, rarely 3-4 × as long as wide).

Type.—Moist shaded rock face, Linville Gorge, 1-1.5 miles below Linville Falls, Burke County, North Carolina, July 28, 1953 (*Schuster and E. F. Jones 28916*). The type material occurred mixed with the moss *Hookeria acutifolia,* and the Hepaticae *Metzgeria hamata, Jubula pennsylvanica, Riccardia multifida.*

In the dentition of the leaves, the narrow cells along the posterior leaf-margin, and the extraordinarily aciculate nature of the dentition of the leaves, this variant closely approaches *P. japonica ciliigera* Schuster, of the Ozarks. The similarities, however, appear to be superficial convergences, not indicating closer relationships, since the following major differences occur: (1) Leaves tardily caducous (persistent in *P. japonica ciliigera*); (2) plants deep green, densely chlorophyllose, with age somewhat bronzed, and often brownish (pale green, pellucid, relatively less chlorophyllose in *P. japonica ciliigera*); (3) leaf-cells smaller, in subapical region of the leaf averaging 21-24 μ, occasionally 23-25 μ wide x 25-30, occasionally 29-36 μ long (in *P. japonica ciliigera* 29-34 μ wide x 35-42, occasionally 48-50 μ long); (4) leaves basically oblong-obovate, with the maximal width normally above the leaf middle (in *P. japonica ciliigera* with leaves basically oblong-ovate, with the width greatest below the middle); (5) oil-bodies coarsely segmented and obviously of the grape-cluster type (in *P. japonica ciliigera* oil-bodies finely and delicately granular or papillose in appearance, formed of minute globules).

Most of the preceding differences also serve to separate *P. sullivantii* (including the var. *spinigera*) from the Appalachian endemic, *P. echinata.* The latter is closely allied to *P. japonica ciliigera.* However, the variation in cell size in *P. sullivantii* is occasionally great enough so that the two species, *P. japonica ciliigera* and *P. echinata* are approached. In three isolated cases,

P. sullivantii showed the apical cells ranging from 21-24 μ to (22) 23-25 μ, and to (23) 25-28 μ. Similarly, the median cells ranged from (22) 23-25 x 25-32 μ up to a maximum of 25-30 x (25) 28-35 μ. The basal cells ranged from 23-25 x 30-40 μ up to 25-29 x 35-45 μ. In each case, the upper figures closely approach the median figures for the *P. japonica ciliigera- P. echinata*-complex. When this abnormally large cell size is correlated with persistent

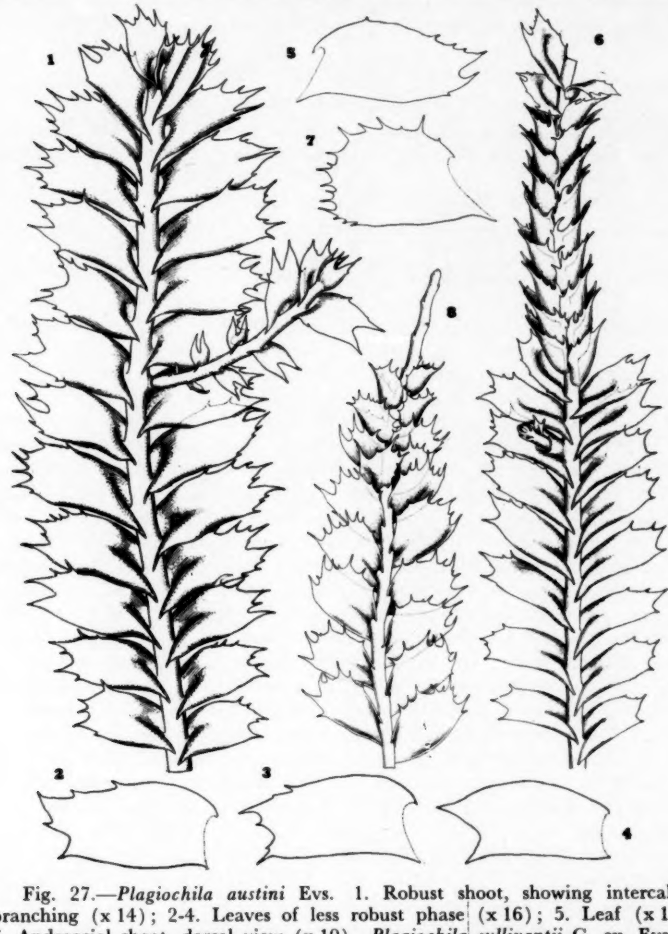

Fig. 27.—*Plagiochila austini* Evs. 1. Robust shoot, showing intercalary branching (x 14); 2-4. Leaves of less robust phase (x 16); 5. Leaf (x 13); 6. Androecial shoot, dorsal view (x 10). *Plagiochila sullivantii* G. ex. Evs. 7. Leaf (x 13); 8. Androecial shoot with caducous distal bracts, postical aspect (x 10). (Fig. 1, Adirondack Preserve, N.Y., *Britton*; 2-4, Soco Falls, N.C., *Schuster;* 5-8, Robinson Creek, N.C., *Anderson* 10501; in Figs. 5-8 both species are portrayed as occurring in intimate admixture, the *P. sullivantii* freely caducous-leaved, the *P. austini* persistent-leaved.)

leaves, and with the maximal degree of development of the spinose marginal teeth, and with lack of pigmentation (as in shade plants, admixed with *Acrobolbus ciliatus* (=*A. rhizophyllus*), *Radula sullivantii*, *Jubula*, collected by Anderson at Lower Rock Bridge, above Bonas Defeat, N. C.) it sometimes becomes very difficult to separate *P. sullivantii* from small forms of *P. echinata*. It should be recalled that the former never has the leaves bilobate at the apex, the latter always has two of the apical teeth elaborated as incipient apical lobes.

PLAGIOCHILA AUSTINI Evans

Figs. 27: 1-6; 28-30

Plagiochila spinulosa Austin, Hep. Bor.-Amer. No. 9, 1873 (not of Dumortier Rec. d'Obs. 15, 1835 = *Jungermannia spinulosa* Dickson, Fasc. Crypt. 2:14, 1801).

Plagiochila sullivantii Evans, Bot. Gaz. 21:191, 1896 (in large part).

Plagiochila sullivantii Stephani, Bull. Herb. Boissier (Ser. 2) 3:335, 1903 (also Spec. Hep. 2:319, 1903).

Plagiochila austini Evans, Rhodora 16:68, 1914.

Plants usually forming a diffuse mat, showing discrete differentiation into a decumbent or appressed, widely spreading, usually diffuse rhizomatous primary system of leafless stems, from which arise (at either some distance, or in crowded patches) the leafy aerial shoot system; plants deep green when young, *becoming bronzed or brownish with age.* Leafy shoots mostly 2-2.5, occasionally 2.8 mm wide, narrower basally; the shoots also narrowed in potentially caducous-leaved (usually terminal) regions. Aerial shoots mostly 0.8-2, occasionally 2.5-3 cm long, exceedingly fragile. Stems wiry and thin, flexuous, brownish with age, *ca.* 180-240 μ thick; branches few, the *aerial shoots simple or subsimple,* when with branches these intercalary from lower half of leaf-axil, occasionally below the androecial region. Rhizoids usually absent on leafy shoots (at their bases only, when present). Leaves *distant to contiguous,* rather polymorphic, those of weak shoots and of androecial shoots usually *largely bilobed,* with only 0-4 supplementary teeth; *those of robust sterile shoots often with 2-7 teeth* (in *addition to the larger, apical primary teeth or lobes*); leaves essentially *narrowly rectangular,* only slightly narrowed basally, *their anterior and posterior margins subparallel,* the basal half of the postical margin scarcely arched; leaf-width subequal nearly throughout leaf-length; leaf *ca.* 510 μ wide x *ca.* 1050 μ long (on small leaves) to (615) 570-790 μ wide x (1350) 1500-1650 μ long to a mamixum of *ca.* 900-950 μ wide x 1750-1850 μ long (*the length averaging ca.* 2.1-2.3 *the width*); leaves spreading laterally in a nearly flat plane, spreading at an angle of *ca.* (55) 60-80° from stem-apex, *inserted by a relatively narrow line of insertion that is only slightly acroscopically arched,* the line of insertion averaging *ca.* 0.3-0.4 the leaf-length; dorsal leaf-base rather short-decurrent, *postical leaf-base scarcely decurrent,* the postical leaf-margin at best very slightly reflexed; antical leaf-margin, at least on basal one-half of leaf, reflexed,

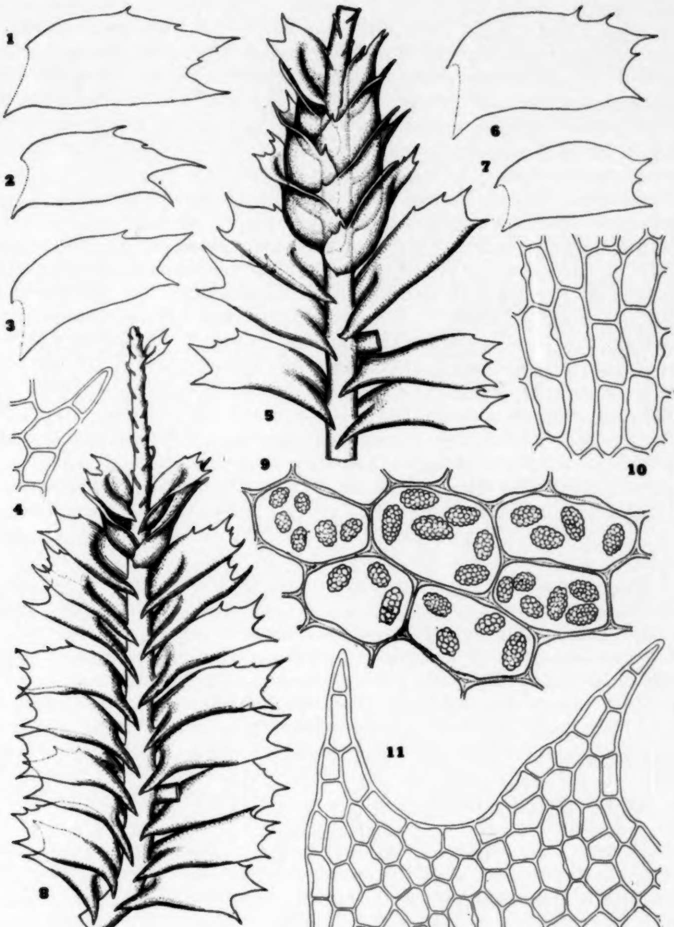

Fig. 28.—*Plagiochila austini* Evs. 1-2. Leaves (x 18); 3. Leaf (x 24); 4. Small tooth from postical leaf-margin (x 230); 5. Sector of androecial plant with upper leaves of androecium caducous; branch cut off at base (x 24); 6. Leaf (x 22); 7. Juvenile leaf (x 18); 8. Shoot, with freely caducous and somewhat aborted male bracts (x 18); 9. Median cells with oil-bodies (x 460); 10. Basal cells from leaf-middle (x 230); 11. Cells of leaf-apex from same leaf from which Fig. 10 was taken, same scale (x 230). (Figs. 1-2, 9, Dry Falls, N.C., *Schuster;* 3, 5-8, *Schuster* 24194, Soco Falls, N.C.; 4, 10-11, *Anderson* 10501, Robinson Creek, N.C.)

but cnemis poorly developed. *Juvenile and branch leaves normally merely bilobed* (to 1/3, the lobes acuminate, with 0-4 small accessory, spinose teeth; mature leaves with the primary bilobing often obscured by the 2-7 accessory, sharp, spinose marginal teeth; marginal teeth relatively narrow and spinose, 2-4 cells long and usually 2, occasionally 3 cells wide at base; *major apical teeth (or lobes) relatively coarse, mostly ca.* 8-10 *cells long and ca.* 6-8 *cells wide at base;* all teeth with *apex often terminated by* 2-3 *cells in a uniseriate row. Cells scarcely collenchymatous,* the intervening walls ± thickened, *frequently with intermediate thickenings,* the trigones often indistinct, often rather large but rarely obviously bulging; median cells *ca.* 20-22 (24) μ wide x 25-30 (*occasionally* 28-37) μ long; interior cells near apex *ca.* 20-22 x 23-27 μ; marginal cells near leaf-apex often strongly elongate, 13-15 μ wide x 25-34 μ long, their external (outer) walls often strongly thick-walled, often encroaching medially on the cell-lumen, rendering this somewhat crescentic; inner walls, and walls at right angles to margin, of the marginal cells slightly to scarcely thick-walled; cells near median base 20-24 (27) μ x 30-45 (55) μ long (averaging 1.5-2 × as long as wide), *not forming a vitta.* Oil-bodies rather large, *ca.* 4 x 6 to 5 x 7-9 μ, occasionally to 7-7.5 x 10-12 μ, opaque, short-ellipsoidal to ovoid, formed of coarse, individually protruding globules (arranged in 3-4, occasionally 5 rows, in surface view), of the "grape-cluster" type, occurring 3-6 per median cell, obscuring much of the lumen. Underleaves usually small, consisting mostly of 2-3 short, uniseriate filaments terminated by slime papillae, occasionally of 4-5 or 6 cilia (then 115-150 μ long), and with a basal width of 3-5 cells. *Asexual reproduction usually present, by means of caducous leaves,* often resulting in extensively denuded stems; upper androecial bracts also with a strong tendency to be caducous.

Male plants only known. Androecia strongly spicate, of 3-5, or often 7-15, pairs of closely approximated, imbricated ventricose bracts, forming a compact, narrowly ellipsoidal or linear spike varying from 850-1000 (1100) μ wide; bracts strongly ventricose, erect except for the spreading tips, otherwise similar to leaves, shallowly bilobed, with (0) 3-6 spinose teeth in addition to the short lobes; antical base dilated, extending nearly across stem, above base with usually 1-2 spinose teeth, beyond which it is normally strongly reflexed; insertion of bracts nearly transverse dorsally, not decurrent.

Type.—"On shaded steep rocks in mountainous regions," presumably from the Catskill Mts., (but possibly from the White Mts.); distributed *in* Austin's Hep. Bor.-Amer. No. 9! In some packets of the type *Radula tenax* is admixed.

Distribution.—*P. austini* has an Appalachian distribution. It rarely occurs below 3000 ft. elevation (and then usually only in the northern portions of its range), and may occur to the summits of the higher peaks in the Southern Appalachians (to *ca.* 6600 feet). Although most often occurring in the rich, moist, densely forested ravines (the Mixed Mesophytic Cove Forest) *P. austini* extends up-

ward altitudinally, and northward latitudinally into the boreal Spruce-Fir Biome. The species is unknown from the restricted Southern Blue Ridge Escarpment Gorges. It has a much more extensive range than the allied and rarer *P. sullivantii* (with which it often occurs in the southern portion of the range).

NEW HAMPSHIRE: "White Mts." (July 1857, ex herb. T. P. James, NYBG!). VERMONT: Oregon Mt., above bridge, Newfane (*Wynne* 1928!; misdetermined by Wynne as *"Bazzania tricrenata"!* NYBG); Brandon (Evans, 1921); Birch Hill, Brandon (*Dutton* 13755 *p.p.!* among *Radula tenax,* 836!, 1285!). MASSACHUSETTS: Face of shaded boulder, Chesterfield Gorge, near W. Chesterfield, Hampshire Co. (*Schuster* 41305, with *Bazzania denudata*). CONNECTICUT: Watertown, 500 ft. (*A. Lorenz,* May 22, 1915!); Colebrook, 700 ft. (*A. Lorenz,* May 5, 1916!) Naugatuck and Redding! (*Evans;* see Evans 1914); Branford (*Evans!*). The material from Naugatuck was distributed, incorrectly labelled "Beacon Falls," *in* Underwood and Cook's Hep. Amer. No. 111, as *"P. spinulosa."* NEW YORK: Woodland Valley (*E. G. Britton!*); Slide Mt., Catskill Mts., Ulster Co. (*E. G. Britton,* June 2, 1901!); Phoenicia to Shokan, Catskills Mts. (*E. G. Britton,* June 1, 1901!); near St. Hubert's Inn, Adirondack Preserve (*E. G. Britton,* Sept. 18-26, 1898, with *Metzgeria pubescens!*); High Peak, Catskills Mts., Ulster Co. (*Peck,* 1866, as *P. spinulosa; Peck,* 1866, admixed with *Metzgeria pubescens!* a few caducous-leaved stems so juvenile that they are virtually inseparable from *P. tridenticulata* although certainly referable to *P. austini*); "Catskill Mts.," Sept. 1879 (NYBG!); Catskill Mts. (*C. F. Austin,* 1875!, NYBG); Little Falls, July 1868 (*sub. P. spinulosa,* NYBG!); Pico Trail near Little Moose Lake, Herkimer Co. (*Haynes* 1564!). PENNSYLVANIA: Canadensis (*Britton and Small,* 1899!). WEST VIRGINIA: Quarry Run (Andrews; *fide* Evans, 1914); Monongalia and Pocahontas Cos. (*fide* Ammons, 1940). VIRGINIA: Mountain Lake, Giles Co. (*Patterson,* 1944!; Patterson, 1954!); Big Cascades near Mountain Lake, Giles Co., 3000 ft. (*Sharp V*-229, *V*-258); Prince George Co. (*fide* Patterson); between Lower and Upper Cascades, near Mountain Lake, Giles Co. (*Schuster* 39871). NORTH CAROLINA: Lower Rock Bridge, above Bonas Defeat, E. Fork Tuckasegee R., 3000 ft. (*Anderson* 10633, trace = fo. *stenophylla,* among *P. sullivantii!*); Chattooga Bluffs, near Highlands, Macon Co., 2700 ft. (*Anderson* 8562, = fo. *stenophylla,* with *Radula sullivantii, Acrobolbus rhizophyllus*); Big Dog Mt., above Dry Falls, Macon Co., 4000 ft. (*Anderson* 9085!); Robinson Creek, near jct. of Slattern Branch, 10 mi. E. of Glenville, Jackson Co., 3200 ft., (*Anderson* 10502, 10501, *p.p.,* with *P. sullivantii!*; plate); Dry Falls, Cullasaja R., NW. of Highlands, Macon Co. (*Anderson* 10323, 10326!; *Schuster* 25215, 25211a, 25229, 25164, 25245, 25211a, 25241a, 25248, 25216 *p. p.,* with *P. sullivantii, P. caduciloba, Herberta sakuraii*); Lloyd's Cove, Scaly Mt., near Highlands, Macon Co., 4200 ft. (*Anderson* 9130 *p.p.,* with *Radula tenax!*); Cane Creek, 8 mi. SE. of Highlands, Macon Co. (*Anderson* 8380!); Soco Falls, near Cherokee, Jackson Co. (*Schuster* 24194, plate!); near summit of Richland Balsam, on E. side of peak, 6400 ft., in Haywood Co. (*Schuster* 39701, c. androecia and caducous leaves); creek running east from Fork Ridge, just above jct. with W. Fork Pigeon R., above jct. with Flat Laurel Creek, *ca.* 4500-4600 ft., S. of Sunburst, Haywood Co. (*Schuster and Bryan* 39379). TENNESSEE: Mt. Le Conte, Sevier Co., 6000 ft. (*Sharp* 34995!); foot of Ramsey Prong, Greenbrier, Sevier Co., 2700 ft. (*Sharp* 3886b!, male, with *Blepharostoma*); Alum Cave Parking Lot, foot of Mt. Le Conte, 4000 ft. (*Sharp* 5164!); Mt. Le Conte, above the Orchard, 3000 ft. (*Sharp* 3576!); Ramsey

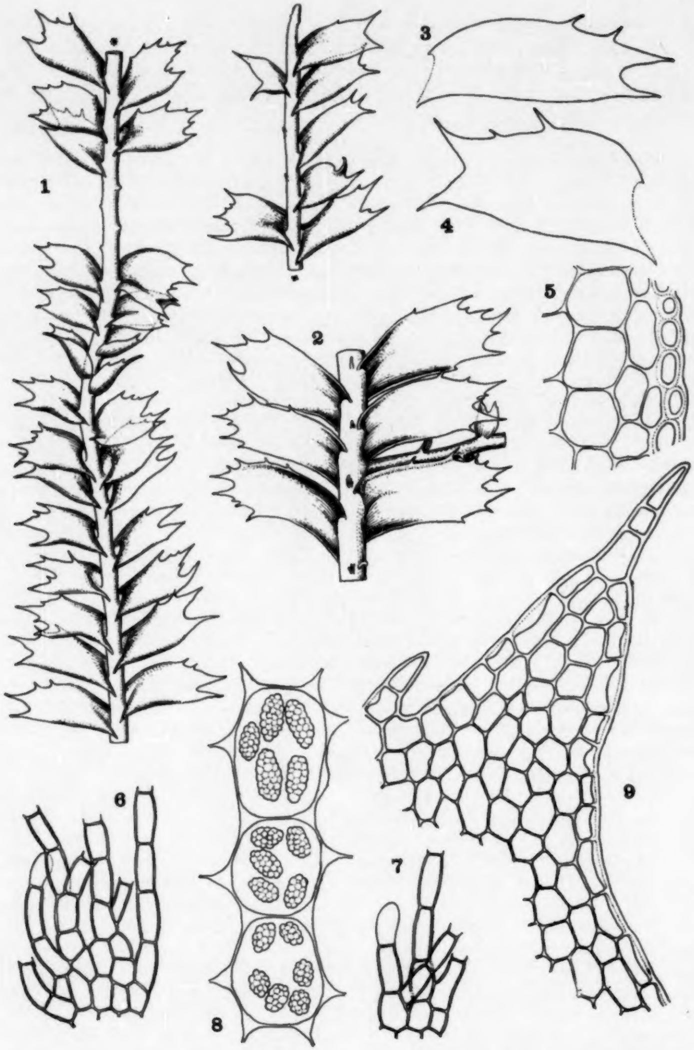

Fig. 29.—*Plagiochila austini* Evs. 1. Medium-sized shoot, with caducous leaves and vestigial androecium (x *ca.* 14); 2. Postical aspect of shoot-sector, showing branching (x *ca.* 20); 3-4. Leaves from leading shoots (x 21); 5. Part of stem cross-section (x 420); 6. Underleaf of maximal size (x 230); 7. Small underleaf (x 230); 8. Median cells with oil-bodies, of mod. with unusually marked trigones (x 625); 9. Leaf-lobe, with cells indicated (x 270). (Figs. 1-2, 6-7 from type, *Austin's* No. 9; 3-4, 8, Dry Falls, N.C., *Schuster;* 9, Soco Falls, N.C., *Schuster* 24194.)

Cascade, Greenbrier, Sevier Co. (*Sharp* 3896 *p.p.!;* with traces *P. sullivantii, Acrobolbus rhizophyllus*); same data (*Sharp* 39117!); Foad Prong, above the Chimneys, Smoky Mts., Sevier Co., 4500 ft. (*Sharp* 36176!); Brushy Mt. Trail from Greenbrier, Sevier Co., 3500 ft. (*Sharp and Voth* 3648!); Roaring Fork, Mt. Le Conte, Sevier Co., 6000 ft. (*Sharp* 3450!); near juncture with Middle Prong of Little R., below Tremont, Blount Co., *ca.* 1600-1800 ft. (*Schuster and Sharp* 34621); along branch of West Fork of Little Pigeon R., above Chimneys Parking Area, *ca.* 4500 ft., Sevier Co. (*Schuster* 35627; 25629a, with *Odontoschisma prostratum;* 25629). OHIO: Cantwell Cliffs, Hocking Co. (*Taylor* 101!).

Ecology.—*P. austini* is an essentially saxicolous species, frequent only on densely shaded, damp (but not wet) rock-walls, where it may form characteristic, pale brown to brownish mats. The species undergoes ecesis only when there is a continuously low saturation deficit, and where only very diffuse light prevails. Occasionally, when there are abundant local saxicolous populations, we find the species invading the lower portions of trees, especially in shaded gorges and near waterfalls—where the saturation deficit, even several feet from the ground, remains exceedingly low at all seasons of the year. Apparently totally absent from calcareous areas.

On shaded damp rock walls, in the Southern Appalachians, the species is often found with *P. sullivantii* and *caduciloba* (as at Dry Falls, North Carolina), often with *Radula sullivantii* nearby, occasionally intermingled with *Herberta sakuraii* and with *Metzgeria hamata.* Less frequently associated are *Blepharostoma trichophyllum, Acrobolbus ciliatus, Bazzania denudata, B. tricrenata,* and *Radula tenax.* With the accumulation of a slight soil layer, *Diplophyllum apiculatum, Microlepidozia sylvatica* and *Lejeunea lamacerina gemminata* may be associated. Very rarely, and apparently only in association with shaded ledges, the species may invade decaying logs (Chattooga Bluff, N. C., *Anderson* 8562); there it may occur with *Radula sullivantii* and *Acrobolbus ciliatus* (= *rhizophyllus*).

Near the northern edges of its range (as in the Catskill and Adirondack Mountains) the local and rare *Metzgeria pubescens* may be associated.

Differentiation.—*P. austini* has had an involved history, detailed by Evans(1914). During the early days of American Hepaticology, it was considered identical with the European Atlantic *P. spinulosa,* which differs at once from our species in the ovate leaves and the cells with large, bulging trigones. When Evans (1896) described *P. sullivantii* he included in his original concept of that species not only the plants we now refer to *sullivantii,* but also the plants now referred to *P. austini,* emphasizing, however, the considerable variability of the species as thus circumscribed. Stephani (1903) soon pointed out that Evans' *P. sullivantii* represented a composite species, and that much of the material Evans referred to the latter did not agree with other plants referred to Gottsche's manuscript species by Evans. Un-

fortunately, Stephani attempted to restrict the name *P. sullivantii* to the plants which we now call *P. austini,* while he applied the manuscript name *P. allegheniensis* Evs. to the plants that were identical with Gottsche's type of *P. sullivantii.* Evans (1914) pointed out that he had clearly typified *P. sullivantii* from the Sullivant material collected in 1845, and that consequently, the application of names in Stephani was incorrect. Consequently *P. allegheniensis* Evs. ex Stephani was placed in synonymy under *P. sullivantii,* and for the plants called *P. sullivantii* Stephani (*nec* Gottsche) the new name *P. austini* was proposed. However, in the NYBG copies of the Stephani Icones, the leaf figured as *Plagiochila allegheniensis* Evs. is clearly subrectangular, over twice as long as wide, and belongs to *P. austini* Evs.

The confusion between these two species emphasizes their close relationship. Indeed, among our species, *P. austini* is clearly related only to *P. sullivantii.* The two species share in common many characteristics (easily and freely caducous leaves, which are very fragile, fragile and filiform stems, a narrow line of insertion of the leaves, a tendency towards brownish color and glossiness, similar size, oil-bodies, stem-morphology, and similar intercalary, monopodial and equally diffuse branching). Evans (1914, p. 70) noted that "the stems and branches are exceedingly fragile, and the leaves readily become detached, especially when dry. Through their regeneration they probably play an important part in the dissemination of the species." The identical condition occurs in *P. sullivantii* although this has not been noted in the literature.

In both *P. austini* and *P. sullivantii* we find occasional mats where no trace of caducous leaves is present. Evidently, although both species share the ability to produce caducous leaves, this "ability" is not expressed under certain environmental conditions. Indeed, the two species differ in the stimuli necessary to initiate production of caducous leaves. This is evident from a study of collections where the two taxa grow intermingled (as in *Anderson* 10501, where the *P. austini* has uniformly persistent leaves, *P. sullivantii* partly caducous leaves).

In fact, except for the differences in leaf-form, the two species are so similar that one is tempted to agree with the earlier statement by Evans (1896, p. 192) where he comments under the discussion of *P. sullivantii* (s. lat., including *P. austini*): "Some of our forms differ considerably from . . . the type of the species; but no good lines of distinction can be drawn between them, as intermediate forms also occur."

However, the differences in leaf form are constant and clear cut. *P. austini* is characterized by leaves usually 1.9-2.3 × as long as wide, often sharply bidentate at the apex, essentially narrowly ovate-rectangular to lingulate-rectangular in shape. The leaves of juvenile shoots or immature (lower) leaves of mature shoots are predominantly bilobed, and characteristically even mature leaves have the two apical teeth larger, forming incipient lobes, with the secondary teeth (usually

2-4) considerably smaller in size. By contrast, *P. sullivantii* has mostly clearly obovate leaves, only infrequently showing an apex divided into two large teeth, and the leaves are usually only 1.4-2.0 × as long as wide. It should be remembered in making measurements of the leaves that juvenile leaves of *P. austini* often are slightly wider than normal, and may be only 1.8-1.9 × as long as wide. It should also be noted that *P. austini* usually has the leaves subrectangular, but may have them widest at the middle or even slightly wider above the middle (narrowly elliptical-rectangular), and they especially appear that way when not dissected off the plants. However, the fewer, coarser teeth of the leaves, the generally evidently bilobed apices of the leaves, and the much narrower form of the leaves serve to separate such plants from *P. sullivantii.*

The writer has been able to discover the two species intimately intermingled, growing with *Bazzania denudata,* etc. (Dry Falls, N. C., *Schuster* 25241), yet retaining all of the evident distinctions, with no tendency towards intergradation at all. The distinctions between juvenile shoots and branch leaves hold particularly well: leaves of *P. austini* being bilobed to one-third, the lobes broad-based and with few or no accessory teeth, whereas in *P. sullivantii* the leaves retain their obovate shape, are divided into 2-4 shallow lobes or coarse spinose teeth.

In Frye and Clark (1944, p. 434) *P. austini* is separated from *P. sullivantii* solely on the basis of the "minute or wanting" trigones of the latter, *vs.* the "moderately large to bulging" trigones of the former. Even though in general *P. austini* has more evident trigones than *P. sullivantii,* this criterion breaks down completely. However, correlated with the more elongate leaf of *P. austini* we find a strong tendency for the median cells of the leaves to be quite elongate and rectangular to elongate-hexagonal, often averaging as much as 25-30, occasionally 28-37 or even 40 μ long, but only 20-22, rarely 24 μ wide; by contrast, the median cells in *P. sullivantii* are less elongate, more nearly isodiametric, and average 23-25 μ wide by 24-28 μ long. Furthermore, *P. austini* has commonly notably elongate marginal cells even at the bases of the chief lobes or teeth, which may be only 13-15 μ wide by 25-34 μ long (averaging twice as long as wide; with the outer walls usually unequally thickened); in *P. sullivantii* the marginal cells except in the spinose teeth, are usually 16-18 μ wide by 21-25 μ long (thus averaging much less than twice as long as wide; furthermore, their outer walls are not or only exceptionally strongly thick-walled). In extreme forms of the species, these distinctions in cell shape and dimension appear to break down.

In the key of Frye and Clark (*loc. cit.*) much of the less robust material of *P. austini* might be sought under *P. tridenticulata,* since the statement "Leaves distinctly 2-lobed for 1/4 - 1/3 their length, occasionally with an additional ventral lobe or teeth" would apply to this material. However, the superior size of *P. austini,* the segmented oil-bodies, and the narrower leaves with virtually straight margins should eliminate all confusion. The two species do agree in their freely caducous leaves.

The androecia of this species have never been described or figured. In the material of *Schuster* 24194, several androecial plants are present. In these the androecia consist of 3-4 pairs of closely imbricate suberect bracts. The bracts

are strongly concave basally, distally are bilobed, with the lobes again usually each with 1-2 teeth; the antical base of each bract is produced as a spinous tooth (rarely with 2 teeth), but this tooth is scarcely produced as a basal lobe; the antical margin beyond the subbasal tooth (or teeth) is often narrowly reflexed. The androecial bracts are only about 2/3 the length of the vegetative leaves below them, and form a short, compact spike-like structure. In some cases, the androecia are not terminal, but end in a slender, caducous-leaved prolongation of the axis that is virtually or completely denudate (Fig. 28:5, 8). In other cases, the formation of androecia does not result in eventual development of caducous leaves (for instance, in *Anderson* 10501; Fig. 27:6). In such cases, the androecia may be prominently elongate, formed of as many as 12-16 pairs of bracts. The androecia in these cases occur on leading shoots, which innovate distally — thus the androecia become intercalary. The bracts in the case of such well-developed androecia differ only slightly from those of caducous-leaved plants, except in a tendency towards development of freer dentition of the bract margins.

Variation.—*P. austini,* like the closely related *P. sullivantii,* appears to be rather stenotypic, again for the reason that it seems able to undergo ecesis only in a limited series of environments. The deep shade, low saturation deficit and sheltered nature of the various ecological niches result in a high degree of uniformity in the species. The major amount of variation lies, in this species as well as in *P. sullivantii,* in the degree to which the accessory spinose teeth of the leaves are produced. When the plants occur in diffuse mats, and the aerial shoots are only 0.8-1.5 cm tall, the plants occur in a somewhat reduced form, in which the leaves of even the main shoots retain certain juvenile features. For instance, the basic bilobate condition remains very evident on all leaves; a high proportion of leaves bear no accessory teeth; other leaves bear usually only 1-4 accessory teeth (1-2 on the distal half of the postical margin; 1-2 in the sinus between the apical lobes). However, when the plants are developed to their most luxurious degree (as is true in the deep mats collected by Britton in the Adirondack Mts., N. Y.), the interwoven, rather dense mat of ascending aerial shoots becomes 2-3.5 cm deep, and the individual shoots more luxuriant. Such shoots bear leaves that are much more fully endowed with marginal, spinose teeth—3-4 teeth occurring on the distal two-thirds of the postical leaf-margin, 2-4 between the apical lobes, and 1-2 on the distal one-fourth of the antical margin. In such cases, the apical lobes may even be obscure, because of the luxurious development of accessory teeth.

The cells of this species undergo only a limited amount of variation. I have seen no extreme leptodermous forms, and conversely, no strongly pachydermous modifications occur. Even when the trigones are relatively small and quite concave, and the intramarginal cells thin-walled, the marginal cells tend to be thick-walled along the external leaf-margins, with the lumen narrowed medially on the individual cells (Fig. 29:9). The elongate or longitudinal walls tend to occasionally produce similar, wide but ill-defined, although salient, intermediate thickenings, even in the more nearly leptodermous forms.

These thickenings become more frequent and pronounced in the forms with barely bulging trigones. With age, and apparently under the driest conditions tolerated by the species, the walls may, in addition, be somewhat evenly thickened.

In addition to the preceding minor (and presumably entirely environmental) variation, *P. austini* occurs as a rare, narrow-leaved extreme.

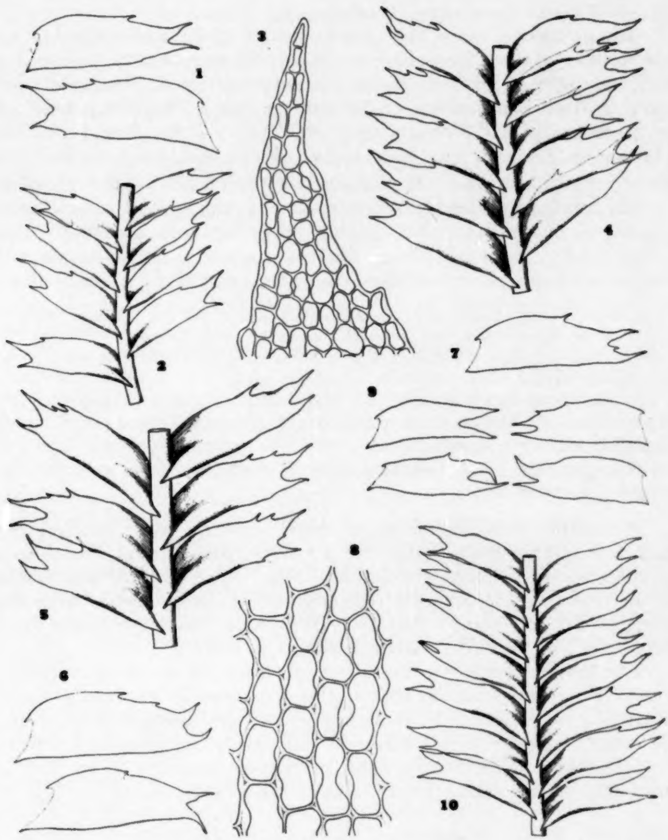

Fig. 30.—*Plagiochila austini* fo. *stenophylla* Schuster. 1, 6-7. Leaves of mature size (x 24); 2. Slender shoot-sector (x 24); 3. Lobe apex (x 170); 4-5. Robust shoot-sectors, antical aspect (x 24); 8. Median cells (x 265); 9. Leaves from smaller shoots (x 24); 10. Medium-sized shoot (x 24). (Figs. 1-8 from *Anderson* 8562, Chattooga Bluff, N.C.; 9-10, *Anderson* 10633.)

P. austini fo. **stenophylla** fo. n.

Fig. 30

P. austinii similis; differt foliis anguste oblongo-linearibus vel oblongo-lanceolatis, *ca.* 2.8-3.1:1; apicibus valde bilobatis, marginibus ventralibus integris vel 1-2-dentatis. Typus: Gorge of Cullasaja R., *ca.* 0.2-0.3 mi. below Cullasaja Falls, on humid, vertical face of large boulder (*Schuster and Schofield* 40737a; in part mixed with *Radula tenax, Plagiochila sharpii, P. echinata*).

Plants slender, *very pale green,* 1.6-1.8 (2.0) mm wide, the aerial shoots very sparsely branched or simple. Leaves remote to contiguous, *narrowly oblong-linear to narrowly ovate-oblong or oblong-lanceolate,* varying from a minimum of 240-260 μ wide x 720-800 μ long up to a maximum of 330-390 μ wide x 960-1100 μ long (*length ca.* 2.8-3.1 *the maximal width*); *leaf-apices normally strongly bilobed,* for 0.15-0.3 their length, the lobes frequently attenuate and briefly acuminate; antical margin entire (rarely unidentate distally), postical margin varying *from entire to 1-2-dentate.* Median cells *ca.* 18-20 μ wide x 30-38 (42) μ long, with ± thickened walls, rounded trigones, and occasionally salient intermediate thickenings of the longitudinal walls.

Type.—NORTH CAROLINA: Gorge of Cullasaja R., 0.2-0.3 mi. below Cullasaja Falls, Macon Co., *ca.* 2200 ft. (*Schuster and Schofield* 40737a). *Paratype.*—Decaying log, Chattooga Bluffs, near Highlands, Macon Co., 2700 ft. (*Anderson* 8562). Type in author's herbarium.

A few plants also admixed with *Plagiochila sullivantii* in *Anderson* 10633 (Lower Rock Bridge, above Bonas Defeat, E. Fork of Tuckasegee R., Jackson Co., 3000 ft., North Carolina).

The paratype plants admixed with *Radula sullivantii* and *Acrobolbus ciliatus* (= *rhizophyllus*).

P. austini stenophylla is the most extreme manifestation of *P. austini* which has been found. It is a well-marked plant, characterized by the extremely narrow, lingulate-linear leaves, the obvious bilobing of the leaf summit, and the reduction of accessory teeth (to a maximum of 2-3, on robust plants). No reason has been found for interpreting this variant as environmental in origin.

The most extreme manifestations of this form are habitually unlike typical *P. austini,* but approach the Japanese *P. trabeculata.* The linear-lingulate, remote leaves, usually obviously bilobed at the summit, are clearly suggestive of the latter. However, the thin-walled cells of *P. trabeculata,* with sharply defined trigones, and the larger size (3-4 mm wide) suggest that the similarities are superficial.

Sectio V: SUBPLANAE Carl

(Sectio Acanthophyllae Carl; new synonymy)

Plants *green, ours never brownish* (exc. *P. rhizophora*), *strongly shining, large or medium sized,* to 5-7 cm long x (1.8-2.8) 3.0-4.5 mm wide, usually very sparsely monopodially branched (or virtually un-

branched), the *branches usually intercalary; nearly or quite prostrate or decumbent in growth;* stolons absent; rhizoids usually few. Leaves *somewhat distant to barely imbricate,* narrow, *lingulate or oblong to rectangulate, to oblong-ovate,* rarely nearly ovate, averaging (1.25) 1.5-3.0 × as long as wide, the *postical base usually not or only inconspicuously dilated* (antical and postical margins thus subparallel for much of their length or only weakly convergent); leaf-margins remotely armed on distal 2/3 or more of postical margin, on apex, and on at least apical part of antical margin with a few (usually 7-15) *sharp, spinose to aciculate, distally linear and uniseriate teeth formed of cells 2-3 (4) times* as long as wide; *postical leaf-base extremely short-decurrent,* not or only exceedingly narrowly reflexed; *antical base ± short-decurrent; leaves spreading horizontally laterally,* inserted at an angle of *ca.* 45-65° to stem-apex. *Cells relatively large and thin-walled,* with small or weak trigones, *ca.* (25) 29-34 μ *wide in leaf-apex* and leaf-middle, subisodiametric; marginal cells often narrow and strongly elongate; oil-bodies (in our species) formed *of numerous small globules, appearing granular or finely papillose* (nearly homogeneous in *P. titibuensis* and *P. pseudopunctata*), 5-8 (9-10) per cell. *Underleaves minute,* of several short cilia. *Asexual reproduction absent,* in our species; in exotic taxa rarely present and via caducous leaves.

Androecia either terminal (and eventually intercalary) on elongate or leading shoots, *occurring singly,* or, *often on abbreviated lateral, intercalary branches* (then frequently produced in some abundance, the leading stems becoming in extreme cases pinnulate with short androecial branches, some of which may originate in the axils of bracts of stem-androecia); androecia narrowly or compactly spicate and becoming more slender distally; bracts in (3) 4-8 (10) pairs, strongly ventricose, the spreading apices and margins with 2 tooth-like lobes and several spinous accessory teeth; monandrous, rarely diandrous. *Antheridia with stalk basically 2-seriate, but through the agency of accessory wall-formation sometimes largely or at least locally 3-4 (-5) seriate.* Perianth terminal on leading stems, with innovations; perianth campanulate-triangular in profile, the keels subequal, unwinged.

The Sectio Subplanae includes here two series of forms: neotropical taxa which fail to show marked tendencies towards elaboration of apical teeth into lobes; and taxa in which the leaf-apices are usually perceptibly bilobed, although the lobes may hardly exceed in size the supplementary, spinous teeth which are always produced. Three species occur in North America, none of which have been previously recognized from this continent. Of these species, two (*P. echinata, P. rhizophora*) belong to the complex which shows elaboration of incipient lobes; these would fall into the Sectio Acanthophyllae of Carl, which was founded for Asiatic species. I prefer to regard the Acanthophyllae as a mere subsectio of the Subplanae, to

which a series of neotropical species have been assigned by Carl. *P. japonica,* the third species represented in North America (by a vicarious subspecies), in some respects appears to show more similarities to the Subplanae than to the Acanthophyllae, *s. str.* Two of our species are endemic, respectively, to the Ozarks and Southern Appalachians; the third is oceanic North Pacific, occurring from Alaska to British Columbia.

The section, as broadly conceived here, is strongly isolated, although in the oblong to oblong-ovate leaves with often parallel sides, most species of the group superficially approach the Cobanae and Parallelae (the latter regionally represented by *P. diffusa*), but no other regional sections of *Plagiochila.* The spinose to aciculate, but strong, remote dentition of the leaves serves to separate this section from any other group of New World Plagiochilae.

Our two eastern species, of restricted and localized occurrence in the Ozark-Ouachita Plateau region and the Southern Appalachians, give the impression of being Tertiary relicts of tropical and oceanic affinity. The most immediate relationship of these taxa appears to be with several neotropical species, *P. hondurensis* Herzog (1932b, p. 204), *P. subplana* and *P. amazonica,* and with the Asiatic *P. japonica.* The relationship appears to be particularly close with the Central American *P. hondurensis.* This latter species differs from the more luxuriant *P. subplana* in its smaller size (6-7 mm wide), and in the narrower leaves. Our representatives of the section in turn differ from *P. hondurensis* in inferior size (2.8-4.2 mm wide). But *P. japonica* subsp. *ciliigera* possesses leaves exceedingly similar in their narrowly lingulate form and aciculate, distant armature of linear teeth. The teeth, in *P. hondurensis,* are, however, often terminated by rhizoids (which is never the case in our species), and are formed (judging from Herzog's fig. 4c, d, e) of less linear cells, though also of 4-6 cells in a uniseriate row. The leaf cells in *P. hondurensis* (36 μ apically, 40 x 60 μ near middle of base) are distinctly larger than in our two species of the section. Of more importance, the marginal cells in *P. hondurensis,* even at the bases of the marginal cilia, are formed of scarcely elongate cells (judging from Herzog's figures). The large size of Herzog's species is correlated with a larger leaf-size (3 mm *vs.* up to 1650-1950 μ long in our species).

Of our two eastern species, one appears to represent an Ozarkian subspecies of a Japanese species. The latter, *P japonica,* in turn exhibits a very immediate relationship with the Asiatic species, *P. acanthophora* Gottsche (from the Indomalayan region) and *P. sciophila* Nees (from the Himalayas). Our other eastern species, *P. echinata,* endemic to the Southern Appalachians, is not closely allied to *P. japonica.* It appears to be related more closely to the Asiatic Sectio Acanthophyllae Carl, as is pointed out under the discussion of *P. echinata.* I question the wisdom of separating the Acanthophyllae from the Subplanae, and for the time being unite them. It is significant that in both groups we generally find no trace of caducous leaves or other modes of vegetative propagation. However, as is emphasized in another connection (p. 349), both

P. japonica and *P. subplana*, respectively assignable to the Acanthophyllae and the Subplanae, produce phases with caducous leaves. In our regionally represented examples of this complex the leaves appear to be uniformly persistent.

In addition to the two eastern representatives, of which adequate material for study has been available, I have seen collections of a plant allied to the Japanese *P. rhizophora*, collected in the Aleutian Islands. This species, in the paucidentate leaves showing a marked tendency towards elaboration of two of the teeth into incipient lobes, closely approaches the Acanthophyllae. *P. rhizophora* further agrees in the large leaf-cells, averaging 25-27 μ wide or more, in the shiny texture, and in the orientation of the leaves. In other respects it is deviant, hence only uncertainly assignable to the Subplanae-Acanthophyllae complex.

The neotropical Subplanae and paleotropical Acanthophyllae, which I regard as members of a single section, agree in most of their more salient features. The large leaf cells, the minute underleaves, the laterally patent, nitid leaves, the lack of propagula, the contiguous, rather than imbricate disposition of the leaves (leaving the stems extensively exposed, when the plant is viewed in postical aspect), and finally the mode of branching are characteristic. As in the Asplenioides, to which the present group is related in the general lack of asexual reproduction, and in the large and relatively pellucid leaf-cells, branching is almost exclusively lateral and intercalary. In *P. echinata* lateral, terminal branches occur very rarely. Similarly, in *P. japonica* isolated terminal branches may be sporadically observed. As has already been noted, a similar "normal" intercalary mode of branching characterizes the Asplenioides, with similar sporadic appearance of isolated terminal branching. It is noteworthy that in *P. echinata* the intercalary branches may originate not only in the "customary" position at the lower end of the leaf-axil, but occur also in various sites away from the leaf-axils. This is the case with the androecial plants shown in Figure 32:12; it also occurs in the type plants, in which branches may originate midway between antical and postical leaf-bases, ventrad of the leaves. As is clear from Figure 32:12, at least some of these irregularly occurring intercalary branches originate from the ventral, rather than the lateral merophytes.

Since the completion of this monograph, Inoue (1958) has treated the Japanese species of this complex, under Carl's sectional name, Acanthophyllae. Inoue and I are in agreement that both *P. rhizophora* and *P. japonica* belong in this complex, which is much better developed in Japan than in North America, with seven species recorded from Japan. Inoue, however, includes three species in the Acanthophyllae, under a Subsectio Belangerianae (Carl) Inoue, which I do not think should be assigned to this section. These are *P. titibuensis*, *P. belangeriana*, and *P. makinoana*. In these species the leaves are narrowly ovate or oblong-ovate, distinctly ampliate at the base, and strongly and consistently narrowed towards the apex, leading to a very different facies, closely approaching that of the Sectio

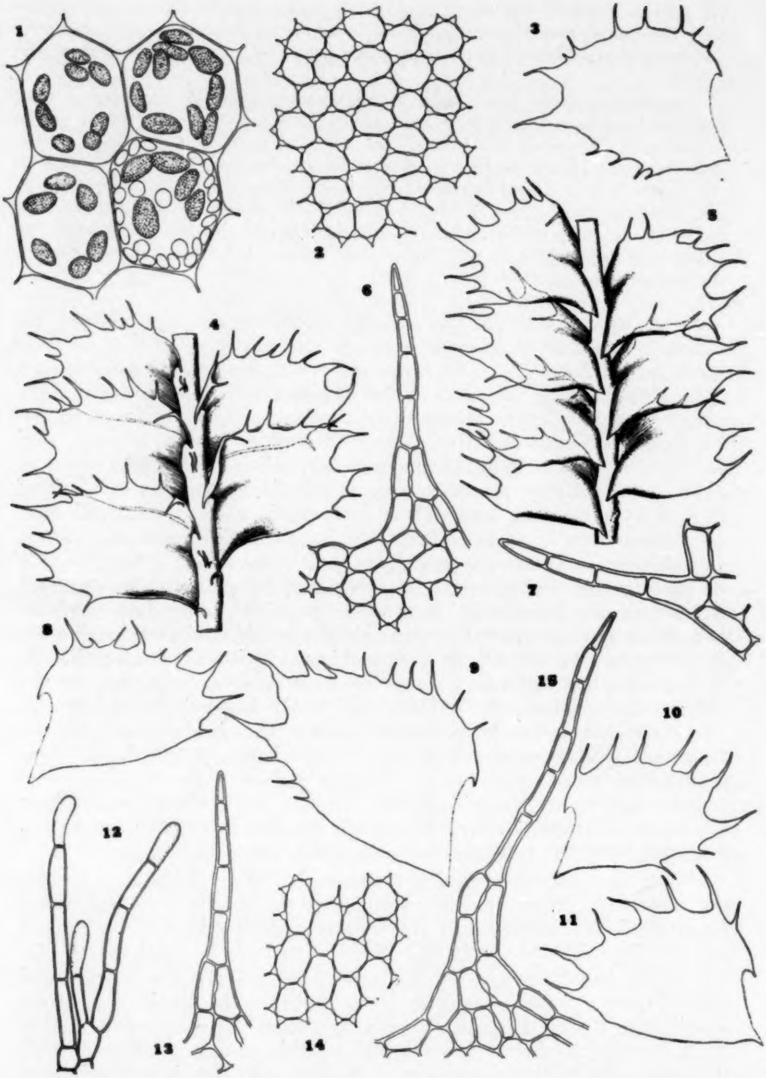

Fig. 31.—*Plagiochila echinata* Schuster. 1. Median cells with oil-bodies, in lower right-hand cell also with chloroplasts indicated (x 530); 2. Median cells

Contiguae. Compare, for example, figs. VI-VII in Inoue with the figures here given of the Contiguae. Furthermore, the cell-size in these three Japanese species shows wide variations, with that of the type species (*P. belangeriana*) only 20 x 20-27 μ in the leaf-middle. This strongly suggests that the Belangerianae should be retained as a group independent of the Acanthophyllae (whether this last group is retained as a distinct sectio or relegated to the rank of a subsectio of the Subplanae), and I therefore cannot follow Inoue in his circumscription of the Acanthophyllae. Inoue (*loc. cit.*, p. 67) lays great weight on the fact that the "structure of the sexual organ(s)" is similar in Acanthophyllae and Belangerianae, hence merges the two. He states (*loc. cit.*, p. 54) that "perianth form, dorsally inflated male bract, and the solitary antheridium are the recognizable characteristics of the section," i.e., the Acanthophyllae *s. lat.*, including *Belangerianae*. Yet *P. echinata* has either 1 or 2 antheridia per bract. This species is very close to *P. euryphyllon* which Inoue, perhaps incorrectly, states seems to be merely a vicariad or form of *P. japonica,* a species he places in the Acanthophyllae *s. str.*

Plagiochila echinata sp. n.

Figs. 31-33

Plagiochila smallii Clebsch (not of Evans), Castanea 19:7, 1954.

Plantae mediocres, pallido-virides, siccae fulgentes; folia patentia, late ovata vel breviter rectangulata, fere plana, apicibus plus minus bilobatis, lobis parvis acuminatis, marginibus dentibus aciculatis vel ciliiformibus, plerumque 8-13, preaditis; dens singulus in filamentum uniseriatum ex 4-6 cellulis angustis (plerumque 3-5:1) compositum contractus; amphigastria minuta, ex 2-5 ciliis brevibus ad basin solam conjunctis composita. Gemmae desunt. Typus: Gorge of Cullasaja River, at about 2200 ft., about 0.2 mi. below Cullasaja Falls, W. side of Gorge (*Schuster* 40736).

Plants medium sized, *loosely prostrate* or loosely pendulous, *not standing* away from substrate, forming *pale green to vivid green* patches, rarely pale brownish; *shiny when dry;* stems, with age, occasionally *becoming ± reddish pigmented.* Shoots simple to very sparsely and irregularly monopodially branched; the branches usually intercalary, from the lower ends of leaf-axils, *very rarely terminal;* some-

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(x 150); 3. Leaf (x 15); 4. Shoot-sector, postical aspect (x 15); 5. Shoot-sector, antical aspect (x 15); 6. Marginal tooth of postical margin (x 150); 7. Cilium from middle of antical margin (x 150); 8-11. Three small and a large leaf (x 20); 12. Underleaf (x 150); 13. Small cilium of postical margin (x 150); 14. Median cells (x 150); 15. Cilium of maximal size (x 150). (Figs. 1-3 from *Schuster and Sharp* 34617, below Tremont, Blount Co., Tenn.; 4-15, from *Anderson* 10539.)

times with numerous short intercalary androecial branches;[4] shoots varying from (2.5) 2.8-3.5 mm wide x (1) 2-3.5 (5) cm long; stems (160) 230-275 μ in diameter, pale brownish-yellow to *reddish-brown with age;* ventral cortical cells *ca.* 14-16(18) μ wide x 35-48(55) μ long; dorsal cortical cells equally wide, somewhat more thick-walled, mostly 40-72 μ long, striolate; rhizoids of leafy shoots occasionally frequent, sometimes absent on leafy shoots, except at base. Leaves ± *laterally patent, dry or wet,* not deflexed, inserted at *ca.* a 50-65 (70°) angle with stem, *short rectangular to ovate-rectangular to broadly ovate* on mature, main stems, polymorphic, varying from 950 μ wide x 1400 μ long to 1100-1220 μ wide x 1450-1600 μ long, up to a maximum of 1300-1375 μ wide x 1600-1700 μ long (*length ca.* 1.23-1.47 × the *maximal width*); leaf-insertion weakly arcuate, the *scarcely dilated postical base very short-decurrent,* the decurrent strip and postical leaf-margin above it narrowly deflexed, thus appearing erect (in postical aspect); postical margin moderately convexly arched, usually with (3) 4-8 spinous teeth; apex almost constantly ± *distinctly bilobed, the lobes acuminate,* often somewhat tortuous, *ending in uniseriate cilia* formed of 5-7 superimposed cells; antical margin *short-decurrent* (the line of insertion of the leaf thus relatively short, varying from 650-1050 μ, i.e., *ca.* 0.5-0.9 the subbasal leaf width), *weakly convexly arched or straight,* bearing (0) 1-3 (4) teeth, usually confined to apical half of margin, but *sometimes with 1-2 (3) small spinous or cilia-like teeth at basal half of margin,* both antical and postical margins deflexed, although never revolute, the leaf thus quite convex; *marginal teeth* (and extensions of the terminal lobes) *spinous and ciliiform,* rather rigid, tapering, prominent, *usually* 8-13 (15) *per leaf,* the longer 2-3 cells wide at base, suddenly contracted into a uniseriate filament formed of 4-6 *narrow, elongated, superimposed cells* (cells averaging (36) 44-58 μ long x 13-16 μ wide, thus mostly 3-5 × as long as wide; occasional cells to 70 μ long). Median and subapical cells hyaline, *rather weakly to distinctly collenchymatous,* with thin walls and small to slightly bulging trigones, averaging (25-27) 28-31 (33) μ wide x 30-35 (38-42) μ long; basal cells very similar, the walls similar, averaging (25-27) 29-33 μ wide x 34-44 (50) μ long, not at all forming a vitta; cells near the margins of mature leaves becoming tangentially elongated (especially along whole postical margin), averaging 35-48 μ long x (13) 15-20 μ wide, thus *often*

[4] This species occasionally shows very free — and irregular — formation of the bud-like androecial branches. These may originate in the traditional site, i.e., from the lower halves of the lateral merophytes, just anterior to the postical leaf-base; they then appear to arise from the lower portion of the leaf-axil. In other cases they arise clearly from the lower margins of the lateral merophytes, from a point directly *under* the leaf. Sometimes their origin is midway between the anterior and posterior leaf-margins; in other cases, they arise just under the postical margin of the leaf; in still other cases, 2, or even 3 of these intercalary branches may arise, closely juxtaposed to each other. Finally, at least occasional intercalary branches are of postical origin. The normal vegetative branches are at least in small part of terminal origin, however.

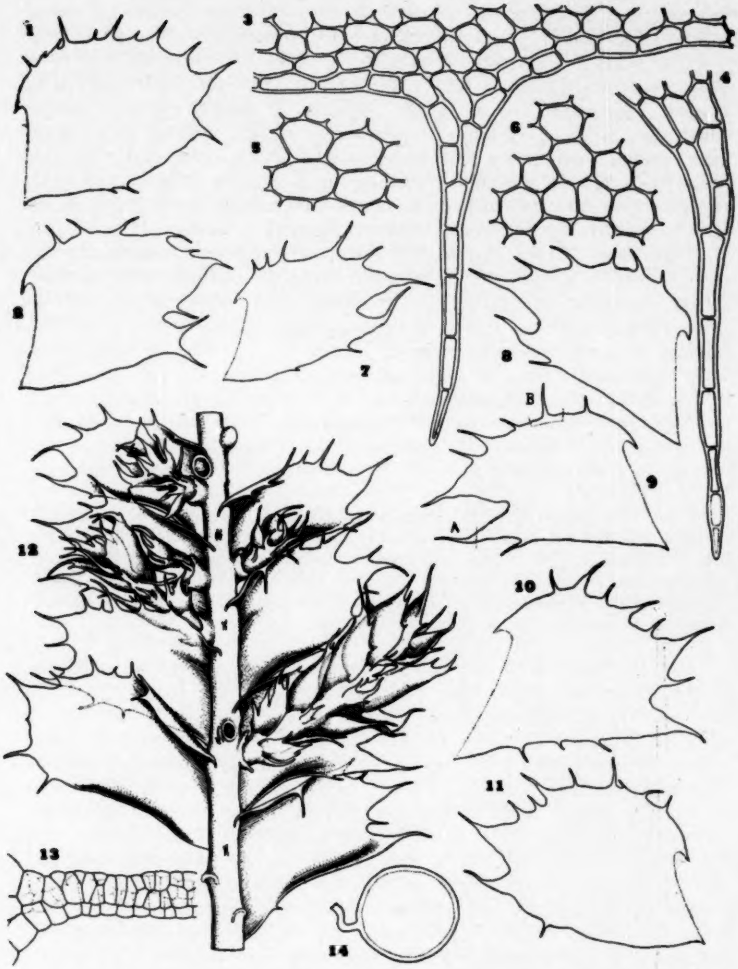

Fig. 32.—*Plagiochila echinata* Schuster. 1-2, 7-11. Leaves, 1-2, 10-11 of maximal size (x 15); 3. Cilium of postical margin (x 190); 4. Apex of terminal leaf lobe (x 190); 5. Basal cells (x 190); 6. Median cells (x 190); 12. Shoot with 7 intercalary androecial innovations (two broken off) and an intercalary "bud," postical view (x 17); 13. Stalk of antheridium (x 190); 14. Antheridium (x 42). (All from *Redfearn and Clebsch* S62, Tennessee; determined by T. C. Frye as "*P. smallii*" and cited as such in Clebsch.)

2-2.5 × as long as wide; cells in leaves generally virtually isodiametric, except along margins, in cilia, and at the very base (where ± elongated). Oil-bodies (4) 5-10 per cell, short-ovoid to ellipsoidal, from 4 x 5 to 4.5-5 x 7-9 μ, occasionally 5-7 x 10-11 μ, *formed of very numerous, extremely minute barely perceptible spherules,* thus appearing opaque, somewhat greyish, finely papillose or nearly smooth; chloroplasts only 4-4.5 (5) μ long. *Underleaves minute,* formed of 2-5 short cilia, united at the very base only, each of 2-5 narrow and elongated cells, each cilium commonly ending in a hyaline papilla. *Asexual reproduction lacking* (unless the brittle and easily fragile teeth of the leaves may be effective as reproductive agents).

Dioecious. Male plants only known. Androecia compactly spicate, 800-1650 μ wide, either terminal on long, leading, leafy branches (then becoming intercalary), or forming sessile, abbreviated bud-like intercalary branches. Bracts strongly saccate, erect, closely imbricate, bilobed at apex, the lobes running out in slender cilia; margins similarly spinose-ciliate; 1-2 androus; antheridia ovoid, 240 x 280 to 320 x 360 μ, the stalk rather long, of at least 2 rows of cells (each row with some or most cells undergoing vertical division: the stalk thus at least locally 4-seriate); bracteoles distinct, bifid to ovate-lanceolate, ending in a cilium, and remotely, sparsely ciliate-dentate on margins.

Type.—On deeply shaded, damp rock-walls and in recesses, gorge of Cullasaja River, 0.2 mi. below Cullasaja Falls, 2200 ft., Macon Co., North Carolina (*Schuster* 40736). Type material in herbaria of author, of Duke University, University of Tennessee, Canadian National Museum, Hans Buch, Naturhistoriska Riksmuseum of Stockholm, Sweden, Herbier Boissier, Hattori Botanical Laboratory, U. S. National Museum.

Distribution.—A species of restricted range, occupying a small area of the gorges along the Blue Ridge Escarpment (at from 1200-2600 ft.), and from similar gorges in the Great Smoky Mountains of adjacent Tennessee (there at 1600-4300 ft.). The plant has a distribution closely paralleling that of the Appalachian endemic, *Mnium carolinianum* Anderson, and the two are found together in the Gorges of the Thompson and Whitewater Rivers. The narrow altitudinal range is remarkable. The plant is closely associated with the *Hymenophyllum-Trichomanis* area of the gorges, in the Mixed Mesophytic (Cove) Forest. In the Estatoe River it is found within 5-10 ft. of the site at which *Hymenophyllum tunbridgense* formerly occurred (the latter now extinct there, or virtually so, through indiscriminate collecting!). It also occurs in the Estatoe with *Trichomanis petersii.* In the Cullasaja Valley it occurs in an area notable for the occurrence of *Hymenophyllum* (Dry Falls, Cullasaja Falls, Crow Creek) and *Trichomanis boschianum* (Crow Creek). It appears most frequent in areas where localized calcareous or subcalcareous conditions obtain.

NORTH CAROLINA: Cullasaja R., about 0.2 mi. below Cullasaja Falls and within 200 yards of the falls, 2200-2400 ft., Macon Co. (*Schuster* 40736, 40743,

40745); moist shaded rock, stream bank, Wolf Creek, near jct. with East Fork of Tuckasegee R., Jackson Co., 2600 ft. (*Anderson* 10195!, 10225!); Upper Falls, Whitewater R., Jackson Co., 2400 ft. (*Anderson* 8647!; also a trace in *Anderson* 8645); below Windy Falls, Horsepasture R., Transylvania Co., 2000 ft. (*Anderson* 8475, 8456, 8453, 8454, 8455); midway between Windy Falls and Rainbow Falls, Horsepasture R., Transylvania Co., 1600-2000 ft., and just below Rainbow Falls, 1400-1600 ft. (*Schuster* 37821, 37830, 37843; *Schuster and Anderson* 34721); Rock Creek, Toxaway Gorge, SW. of Rosman, moist rocks at edge of stream, 1200 ft. (*Anderson* 12895!); moist shaded bluff, N. face, 1200 ft., Cane Brake, Toxaway R., SW. of Rosman, Transylvania Co. (*Anderson* 12857!). TENNESSEE: near first bridge, Porter's Flat Trail, Greenbrier, 2500 ft., Sevier Co. (*Redfearn and Clebsch,* SM 62!; determined by Frye as *P. smallii,* and reported as this by Clebsch, 1954); shaded rocks near falls below Tremont, Blount Co., 1600 ft. (Sharp 34216!; scrappy, but clearly this species; reported by Sharp, 1939, as *P. sullivantii;* same locality, *Schuster and Sharp* 34617); Mt. Le Conte, on moist rock, Sevier Co., 4300 ft. (*Sharp,* Feb. 14, 1932, as *P. sullivantii!*); left prong of river above Greenbrier, Sevier Co. (*Sharp* 3870b, Apr. 24, 1938, as *P. austini*); above the Orchard, Mt. Le Conte, Sevier Co., 3000 ft. (*Sharp* 3566, 3574, as *P. austini, in* Sharp, 1939); Ekaneethee Creek, Cades Cove, Blount Co. (*Sharp* 34746, as *P. austini in* Sharp, 1939; material fragmentary and doubtful); Abrams Falls, Cades Cove, Blount Co., 1800 ft. (*Sharp* 127, 1932; Yale, as *P. sullivantii*); W. of Elkmont, Sevier Co. (*Sharp* 108, 1931; as *P. sullivantii?*); Falls Trail, Mt. Le Conte, Sevier Co., 4500 ft. (*Sharp* 136, 1932; as *P. sullivantii*). SOUTH CAROLINA: Thompson R., NE. of Jocassee, Oconee Co. (*Schuster* 40970, 40978; *Anderson* 10539); Estatoe R., Pickens Co., variously in lower part of gorge, at the "Narrows," and along a west branch lying below the "Narrows" (*Schuster* 37625, 37624, 37622, 37624a, etc.); along Laurel Fork, W. of Rocky Bottom, 1200 ft., on moist shaded rocks (*Anderson* 12877!).

The preceding material has been labelled as cotypic and paratypic, except in those instances where the plants are fragmentary or juvenile.

Ecology.—*P. echinata* has much the same ecological requirements as *P. austini* and *P. sullivantii,* growing chiefly in moist, deeply shaded recesses or deep crevices of vertical rock walls, in areas never touched by direct sunlight, and often in areas near rapidly flowing water. Indeed, the species rarely occurs far from waterfalls.

The plant, however, is even more restricted ecologically than *P. austini* and *sullivantii.* It appears more strongly restricted in occurrence by a sharper dependency on high humidity, occurring largely near waterfalls, or on seepage-moistened rocks. It is particularly frequent on the undersurface of projecting ledges, in deep shade, associated with waterfalls. This, of course, is the habitat of *Hymenophyllum tunbridgense,* with which it was consociated in the Estatoe R., before extinction of the *Hymenophyllum.* Often with *Trichomanis petersii* (both in Tennessee and in South Carolina). Associated on such shaded, damp ledges are most often *Radula sullivantii, Mnium carolinianum* (an Appalachian endemic with a strikingly similar range!), *Calypogeia muelleriana, Jubula pennsylvanica, Porella pinnata* var. (a most characteristic variant, or perhaps distinct species,

with repand-dentate leaves and ciliate underleaves). On the least sheltered sites, as on the vertical faces of damp boulders, sometimes with *Radula obconica* and *Plagiochila virginica* (and the var. *caroliniana*), occasionally with *Lejeunea laetevirens*. At the type locality most of these taxa are consociated, as well as *Plagiochila sharpii, P. caduciloba, P. austini stenophylla.*

The material collected by the writer is often poorly developed and gives the impression of representing populations in immediate danger of extinction. It is probable that lumbering, which was extensive in both the Estatoe R. and in the Horsepasture R., as well as in the Blount Co., Tenn. station, served to "open up" the ravines to which the species is limited, reducing the humidity and increasing insolation. In Tennessee, the Blount Co. station was reduced to an extremely sparse population. Dr. Sharp, who collected the species there before lumbering occurred, recalled (in conversation) that the plant was at one time common there. As a consequence, *P. echinata* is in somewhat the same danger of extinction regionally as is *Hymenophyllum*. An exception is formed by the type station, where the species occurs very locally, but at one place abundantly, forming in parts pure mats a foot or more across. The plant exists here under apparently optimal conditions, on thinly soil-covered rocks, often admixed with mosses. The well-developed male plants found in the Thompson R. gorge (*Schuster* 40970) also were found over thinly soil-covered vertical faces of ledges and large boulders, associated with several mosses (*Cirriphyllum bosci, Thuyidium delicatulum, Plagiothecium, Brachythecium*) and hepatics (*Radula obconica, R. tenax, R. sullivantii, Jubula pennsylvanica*); they occurred in large, luxuriant sheets, sometimes several feet across, in densely shaded sites.

Differentiation.—*P. echinata* closely agrees with the Subplanae in (a) the large leaf cells (on mature leaves averaging 26-30 μ wide) with rather small trigones; (b) the few but strongly aciculate, narrow-based, uniseriate teeth of the leaves, formed of prominently elongated cells; (c) the weakly ampliate leaves, with the postical base notably short-decurrent; (d) the ovate to oblong-ovate leaves; (e) lack of any type of asexual reproduction; (f) the minute underleaves, consisting of 2-several cilia that are connate only at their very bases; (g) the relatively flat leaves, strongly shiny when dry, pellucid and green in color, which are laterally patent both when dry and when moist, remaining nearly flat in drying. The species is also characterized by being uniformly prostrate or procumbent in growth.

The distinctly bifid leaves (*i.e.,* with 2 of the "teeth" at the apex commonly prominent and longly drawn out), the very short leaves, and the occasional tendency for formation of 1-3 short aciculate teeth of the antical margin serve to separate *P. echinata* from all of the Subplanae known to me. These three features at once separate the species from *P. subplana* Lindenb., *P. amazonica* Spr., *P. hondurensis* Herz., *P. leptodictyon* Herz., and *P. japonica* subsp. *ciliigera* Schuster. In all five of these species the marginal cilia of the leaves are much less polymorphous, *i.e.,* more uniform in size and shape. In the elaboration of two of the apical teeth, *P. echinata* clearly approaches the paleotropic Sectio Acanthophyllae of Carl (1931).

The relationships of *P. echinata* are particularly close to the Ozarkian endemic, *P. japonica* subsp. *ciliigera*. However, *P. echinata* has much shorter leaves, on mature shoots usually 1.25-1.4 × as long as wide (averaging 1.75-2.2 × in *ciliigera*), and has leaves that are more ovate, rather than rectangulate. This is particularly evident when the contours of the postical leaf-margins of the two species are compared. In *P. echinata* the postical leaf-margin is quite distinctly arched; in *ciliigera* it is nearly straight and typically almost parallel with the similarly straight antical margin. These differences are sufficiently marked so that it seems impossible to consider these two taxa as conspecific.

A cotype collection of *P. echinata* was reported as *P. smallii* Evs. (= *P. diffusa* Steph.) from Tennessee (Clebsch, 1954), based on a determination made by T. C. Frye (Apr. 13, 1950, *fide* the cotype specimen). *P. echinata* differs from *P. diffusa* in so many respects (absence of asexual reproduction; much larger cells; lack of strong tangential, intramarginal thickening of the

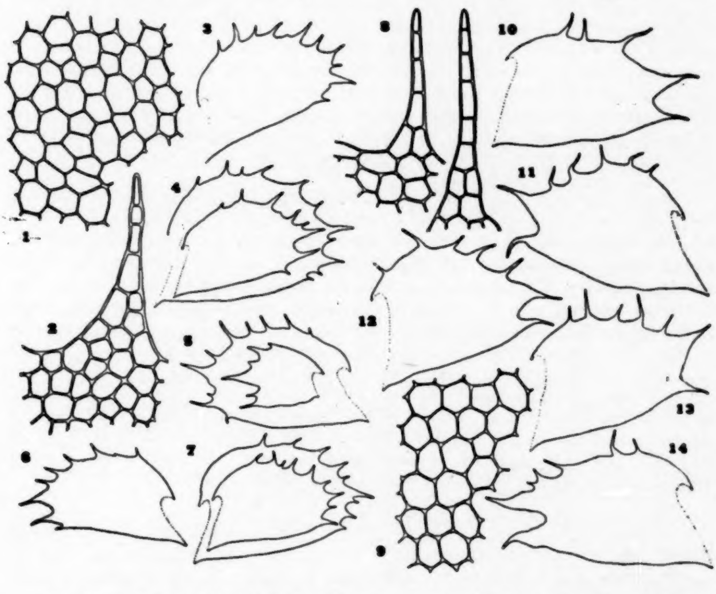

Fig. 33.—*Plagiochila echinata* Schuster; mod. *parvifolia*, largely with cells abnormally small (owing to difficult nutritional conditions?). 1. Median cells, 25-30 μ wide x 25-32 μ long (x 148); 2. Cilium of postical margin (x 148); 3-7. Leaves, in figs. 4-5, 7, branch leaves drawn inside the figures of stem leaves (x 17); 8. Two cilia from postical margin (x 148); 9. Median cells (x 148); 10-14. Leaves (x 17). (Figs. 1-5, 7, from *Anderson* 8647; fig. 6 from *Anderson* 8645; figs. 8-14 from *Anderson* 10195; all from plants collected in North Carolina.)

marginal cells; much more abbreviated leaves, with a fundamentally different dentition; virtual lack of terminal branching) that a closer comparison would be wholly pointless. The two plants belong to unrelated sections.

The cotypes of Anderson, from North Carolina, in contrast, had been determined (Duke Herb.) as *P. sullivantii,* to which *P. echinata* bears considerable resemblance. Both species are shiny, possess leaves that are laterally ± patent when either moist or dry, both have sparsely spinose leaf-margins and relatively abbreviated leaves. Furthermore, the lower half of the postical leaf-margin may be rather broadly reflexed in *P. echinata,* with the consequence that the leaves, *in situ,* may superficially appear to be obovate in shape. However, all of the collections of *P. echinata* lack caducous leaves; they have leaves that are obviously ovate or oblong-ovate (widest subbasally) when flattened out; they possess generally more aciculate teeth of the leaves; they have somewhat larger cells; and they lack the tendency towards formation of a brownish secondary pigment. In the small, leptodermous, extreme shade forms (mod. *leptoderma-parvifolia*) of *P. echinata* some of these distinctions break down. For instance, the small and poorly developed plants from the Whitewater R. (*Anderson* 8647, 8645) have the leaves scarcely more spinous-dentate than *P. sullivantii.* They tend to have unusually small cells, averaging merely (21) 22-25 μ wide in some cases, in others (22) 25-27 (31) μ wide x 26-32 (34) μ long. On the basis of the leaf-dimensions, the dentition, and the shiny appearance, these plants might readily be considered to represent non-caducous leaved *P. sullivantii,* with which they were initially placed. However, the leaves are clearly ovate-oblong in most instances, and never distinctly obovate. Admittedly, the identification of such poorly developed shade forms will remain a matter of considerable difficulty, particularly when the distinctions offered by the oil-bodies cannot be used.

The plants from Tennessee, collected by Sharp, had also been determined in part as *P. sullivantii.* In part they approach this species very closely, particularly Sharp's collection (Feb. 14, 1932), from Mt. Le Conte. These plants are in part xeromorphic, and slightly brownish tinged; they bear obviously bulging trigones. In the tendency towards brownish pigmentation they show a further approach to *P. sullivantii.* However, the ovate leaf-form, and the markedly more spinous-ciliate leaf-margins, as well as the larger leaf-cells serve to identify such material. One feature characterizes these plants, and all the others seen of *P. echinata,* which may help in distinguishing *P. echinata* from *P. sullivantii.* In *P. echinata* the markedly spinous teeth are well developed to within the basal fourth of the postical margin — one or two aciculate teeth always occurring in the proximal half of the postical margin (at least on mature leaves). By contrast, *P. sullivantii* has the basal half of the postical margin usually entire, rarely provided with a solitary tooth.

Although *P. echinata* is sharply isolated from all other North American species, it bears at least superficial relationships to *P. euryphyllon* Carl (1931, p. 106, *nomen nudum*) ex Herzog (1938, p. 232, fig. 8a-e), and has almost an identical leaf-shape, with strikingly similar ciliate leaf-margins. This species, known only from Foochow (Futschau), China, belongs, according to Carl to one of his "Paleotropic" Sections, the Acanthophyllae. If *P. echinata* is keyed out amidst the "Paleotropic" Sections, it will key readily to the Acanthophyllae. *P. echinata* agrees basically in leaf form with such Acanthophyllae as the Japanese *P. sciophila* (see Carl, 1931, fig. 10e), and

is a very close match for the Chinese *P. euryphyllon* (Herzog, 1938, fig. 8a-e), as we have already seen. The tendency of the two apical cilia of the leaf to be elaborated as two small lobes, a tendency emphasized by Carl as diagnostic of this section, is readily evident in *P. echinata.* The postical margin in *P. echinata* is also sparingly armed with cilia that run out into uniseriate filaments; this is also regarded as characteristic of the Acanthophyllae by Carl. Furthermore, Carl emphasizes the "zarte, apikal isodiametrische Zellnetz" of the group; the flat distichous orientation of the leaves; the contiguous and rarely more obviously imbricate disposition of the leaves; and the simple or sparingly branched stems. All of these features suggest *P. echinata.* As a consequence, should it prove wise to recognize the Acanthophyllae, it may be necessary to separate *P. echinata* from the Subplanae, and from the vicinity of *P. japonica ciliigera,* and place it in the oriental Acanthophyllae, which range from Java and the Celebes to Japan, the Sikkim-Himalaya and China. Surely its most immediate affinities are with this complex, rather than with *P. japonica.*

It may prove necessary to reduce *P. echinata* to a subspecies of *P. euryphyllon.* Compare, for example, Figure 31:4 with Herzog (1938, fig. 8a) and Figure 32: 1-2, 7-11 with Herzog (1938, fig. 8b) and Figure 32:4 with Herzog's fig. 8c. However, our plant has smaller leaves (1400-1700 μ long); the Chinese plant has them 2000 μ long. The Appalachian plant has the cilia rigid; Herzog describes them in the Chinese as "ciliis longis flaccidis, saepius hamatis." The Appalachian plant on large leaves (1500-1700 μ long) tends to have 2-3, rarely 4 cilia per antical margin (Figs. 31:3, 9:32: 1,10), while the Chinese plant is illustrated and described with the antical margin as "nudo vel sub apice unispino" although the plant is much more robust and luxuriantly developed. In the closely allied Chinese plant the perichaetial bracts are identical in shape to the leaves, although hardly larger (judging from Herzog's figures); they differ only in the more copious and longer ciliate-laciniate teeth of the postical margin. The juvenile perianth has the broadly rounded mouth longly laciniate, with flaccid laciniae running out into cilia. Unfortunately, the Appalachian plant is totally lacking gynoecia.

It is of some interest that Herzog (*loc. cit.*, p. 233) emphasizes that *P. euryphyllon* is allied to *P. japonica.* I originally considered *P. echinata* (the American vicariad of *P. euryphyllon*) as distinctly allied to what was originally called in manuscript *P. ciliigera,* but was later more conservatively placed as a subspecies of *P. japonica!* Since *P. japonica* and the subspecies *ciliigera* show unmistakable relationships to the Subplanae, it is clear that the Acanthophyllae and Subplanae should be placed in close proximity. The "geographischer Gesichtpunkt" of Carl obscures such an intimate relationship. The immediacy of the relationship is further evident from a consideration of the asexual reproductive modes found in the Japanese *P. japonica* (of the paleotropic Acanthophyllae, according to Herzog) and in *P. subplana* (the type species of the neotropic Subplanae). Hattori has described a caducous-leaved phase of *P. japonica,* discussed under that species; Herzog (1952, p. 68) has

described a *P. subplana* var. *scoposa* provided with "abfallenden Blättchen besetzte Enden auslaufenden ♂-ähren." Evidently both the Acanthophyllae and Subplanae may, if admittedly rarely, reproduce by caducous leaves, although Carl (1931) nowhere mentions the occurrence of caducous leaves in this complex.

In the type collection of *P. echinata* isolated stems show strong reddish-brown coloration. On careful examination it is seen that the pigmentation is not confined to the cortical cells but the medullary cells are similarly colored. There is also a tendency for the cells to separate, when cross-sections are cut, suggesting the coloration is associated with decay of the pectic layer. Why only certain stems show this striking color change is unknown. In some of the material of this collection there are also plants in which the cilia end in thin-walled cells, in part collapsed, which appear to be old slime papillae. In this regard the type plants represent an approach to *P. hondurensis,* although the terminal cells never are in the form of rhizoids.

PLAGIOCHILA JAPONICA Sde. Lac. ex Miquel.
Figs. 34-36

Plagiochila japonica Sande Lacoste *in* Miquel, Ann. Mus. Bot. Lugd.-Bat. 1:290, 1863-64; Mitten, Trans. Linn. Soc. London, Ser. 2, 3:194, 1891; Stephani, Bull. Herb. Boissier 5:81, 1897; Makino, Bot. Mag. Tokyo 11:39, 1897; Inoue, Bot. Mag. Tokyo 15:182, 1901; Stephani, Spec. Hep. 2:298, 1903; Nakanisiki, Bot. Mag. Tokyo 22:64, 1906; Ishiba, Bot. Mag. Tokyo 21:45, 1907; Horikawa, J. Sci. Hiroshima Univ. Ser. B, Div. 2, 2:161, 1934; Kamimura, J. Jap. Bot. 15:67, 1939; Hattori, Nat. Sci. and Mus. (Tokyo) 14:166, Fig. 8, 1943; Hattori, Bull. Tokyo Sci. Museum 11:54, Fig. 30-33, 1944; Hattori, J. Hattori Bot. Lab. No. 3:25, 1948; Hattori, J. Hattori Bot. Lab. 5:77, Pl. I:27-29, Pl. III:51, Pl. VI:14, 1951; Hattori, J. Hattori Bot. Lab. 8: 21, 1952; Inoue, J. Hattori Bot. Lab. 20:55, figs. I:1-17, II:13-17, 1958.

Plagiochila paucispina Steph., MS (*fide* Hattori, 1944).

Plagiochila yokohamensis Steph., MS (*fide* Hattori, 1944).

Plagiochila sciophila Schiffner, Österr. Bot. Zeitschr. 49:390, 1899 (quod plant. Japon., *fide* Hattori, 1952:22).

Plagiochila ferriena Stephani, Spec. Hep. 2:288, 1902; Dugas, Ann. Sci. Nat. Ser. 10 (Bot.), 11:41, fig. 3a, 1929.

Plagiochila paucispina Stephani, Spec. Hep. 6:201, 1921.

Plagiochila acanthophylla Herzog., *in* Verdoorn, Hep. Select. et Crit. (Exsic.), Ser. 7, No. 311.

Plagiochila quadriseta Steph., Spec. Hep. 6:201, 1921.

Plagiochila ciliata Kamimura, Acta Phytotax. Geobot. 14:110, fig. 3, 1952 (non Gottsche; later homonym).

Plagiochila minutistipulata Herzog, J. Hattori Bot. Lab. 14:34, fig. 4a-e, 1955.

Plagiochila japonica has been considered to be an endemic of Japan (Honshu, Kyushu, Shikoku, Yakushima, Hokkaido), and the immediately peripheral regions (Bonin Islands; the Liukiu Islands) of

oceanic Asia. Closely allied plants (*P. acanthophora* Gottsche, *P. sciophila* Nees) are known from the Indomalaya and Himalayas. According to Hattori (1952) these may prove identical with *P. japonica.* Judging in part from a series of Japanese specimens, in part from the descriptions and illustrations of Hattori (1944), *P. japonica s. str.,* is a very variable taxon. The majority of forms seen (typical *japonica;* fo. *oblongifolia* Hattori; fo. *robusta*) are relatively large plants, usually 3.5-5.5 mm wide, with persistent leaves. These plants are further characterized by a peculiarly strongly glistening cuticle (when dry), by a generally pellucid green coloration, by the very sharply spinose-dentate to aciculate-dentate leaf-margins, and, in particular, by the inability to develop caducous leaves. In all of these respects, these manifestations of *P. japonica* agree with the subspecies *ciliigera,* described subsequently, from North America.

In contrast to both the foregoing, more or less typical variants of *P. japonica s. str.,* and to the subsp. *ciliigera,* stands a Japanese plant described by Hattori (1944, p. 55, fig. 31) as *P. japonica* fo. *fragilis* Hattori. Material of it was distributed in Hattori's Hep. Jap. No. 178. This plant is much smaller, less than 2 mm wide, has subquadrate leaves with the dentition usually reduced and less aciculate, usually exhibits a strong brownish pigmentation, and freely drops its leaves — leaving long stem-sectors denuded. This extreme form, if truly conspecific with *P. japonica,* raises difficult systematic problems. *P. japonica,* except for the fo. *fragilis,* shows a clear affinity with the neotropical species of the Sectio Subplanae. This similarity is particularly marked in the subsp. *ciliigera.* By contrast, in its more quadrate to oblong leaves, the ability to drop the leaves, and the strong tendency towards brownish pigmentation, the fo. *fragilis* approaches the species of the Section Choachinae. A solution as to the status of the fo. *fragilis* and of the effect of this on the position to which *P. japonica* will eventually be assigned, must await study of a long series of Oriental specimens, not available to the western student. The ability to produce caducous leaves, *per se,* is of only secondary significance, since forms of *P. subplana* also drop their leaves.

Excluding for the moment the deviant caducous-leaved forma *fragilis,* we may divide *P. japonica* into two subspecies, as follows:

1. Leaves of main stems clearly ovate in most cases, widest in the basal fourth, the postical margin clearly convexly arcuate (leaves of branches, and of weak shoots, often much less ampliate, sometimes clearly oblong or oblong-ovate); leaf-length to width usually 1.25-1.55.... *P. japonica* subsp. *japonica*
1. Leaves of main stems oblong to lingulate, exceptionally slightly ovate-lingulate, virtually parallel-sided, the postical margin slightly convex; leaf-length to width usually (1.75) 1.9-2.1.................... *P. japonica* subsp. *ciliigera*

PLAGIOCHILA JAPONICA subsp. JAPONICA Sande Lacoste
Fig. 34:8-16

The synonymy and distribution cited under the species applies to the present subspecies.

The typical subspecies *japonica* has been repeatedly described and

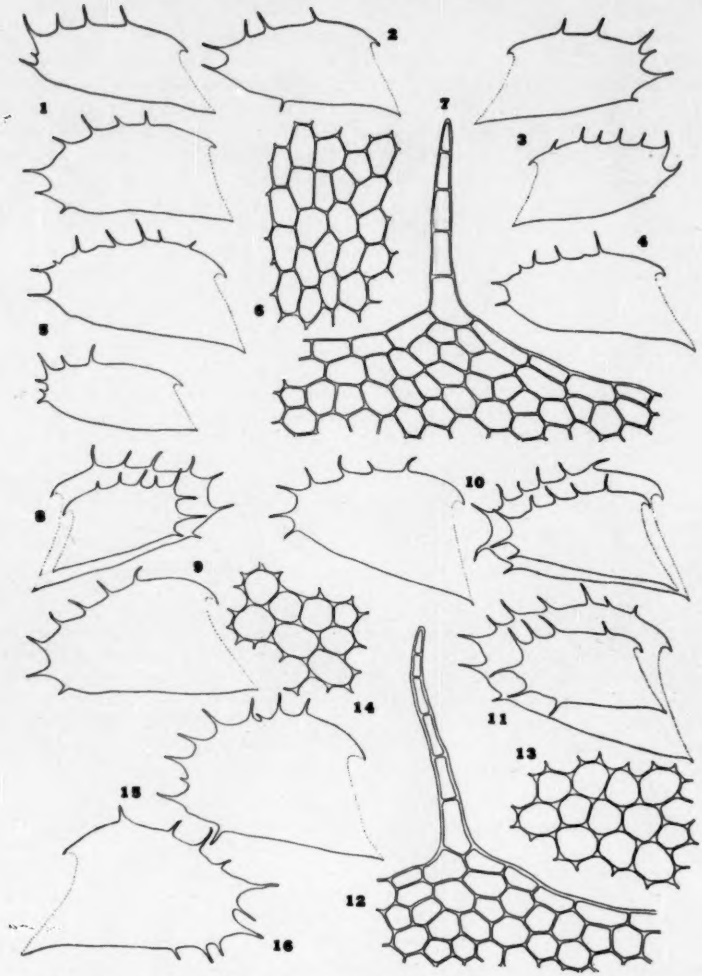

Fig. 34.—*Plagiochila japonica* subsp. *ciliigera* Schuster. 1-5. Leaves, the lower leaf in 5 a branch leaf (x 14); 6. Median cells (x 150); 7. Cilium and leaf-margin along middle of postical margin (x 150). *P. japonica* subsp. *japonica* Sande Lac. 8-11. Leaves, those drawn within figs. 8 and 11 branch leaves (x 14); 12. Cells along postical margin of leaf (x 150); 13. Median cells (x 150); 14. Median cells (x 150); 15-16. Leaves (x 14). (Figs. 1-7 drawn from cotype specimen, from Arkansas, *McGregor* 5413; 8-13 drawn from Japanese plants, *Ikegami* 13466; 14-16 drawn from Japanese plants, *Hattori,* June 1953; all leaf figures drawn to one scale; all cell drawings drawn to one scale.)

illustrated (see particularly Hattori, 1944; and Inoue, 1958). Good comparative material has been distributed by Hattori, in the Hepaticae Japonicae. A comparative study of these (and other Japanese) specimens has demonstrated that these plants are characterized by a fundamentally ovate shape (Fig. 34:8-11, 15-16). Associated with this is a less elongated leaf-form (length: width *ca.* 1.25-1.55:1). Exceptionally (fo. *oblongifolia* Hattori) the leaf-length: width ratio attains *ca.* 2.0:1, yet the leaf retains clear indications of the ovate shape (see Hattori, 1944, fig. 32; Inoue, 1958, fig. 1:18-22). Only on branch-leaves, on the lower leaves of main shoots, or on unusually weak or etiolated stems does the subsp. *japonica* develop clearly oblong leaves. Such branch leaves are contrasted (Fig. 34:8-11) with the larger leaves of main stems, clearly showing the difference in shape. Such branch leaves may approach those of the subsp. *ciliigera* (Fig. 34: 1-5) but are always clearly less elongated in shape.

The variations in leaf-shape, and in dimension, appear to be the only reliable differences that separate the Oriental, typical, race of *P. japonica* from the nearctic race described below. Inversely, the striking over-all similarity of the more typical Japanese plants to the nearctic phase must be stressed. This is so close that, initially, it was felt that a subspecific separation would be both pointless and impossible to maintain. The extreme similarity of the plants extends to the number, size and particularly form of the oil-bodies. Indeed, blinded by the ability of the Japanese phase to produce caducous leaves, the writer at one time did not recognize the close similarity of the Japanese and nearctic plants. It was only after the extreme similarity of the oil-bodies (illustrated for the subsp. *japonica* by Hattori, 1951) was recognized that the possibility of an intimate relationship between the two taxa became clear. It should be stressed that *P. japonica, s. lat.,* has unusually fine-segmented oil-bodies, the unusually minute constituent spherules being surrounded by a relatively firm cytoplasmic membrane. As a consequence, the oil-bodies appear to be faintly granular or papillose, with a virtually smooth surface. A clearer example of the great value of Hattori's excellent work on the cytology of the Japanese species could scarcely be desired.

If the fo. *fragilis* can be shown to intergrade with subsp. *japonica,* a further, more important distinction will apply, since none of the thousands of nearctic plants studied have shown any tendency to drop the leaves. Unlike the Japanese phase of the species, the nearctic form does not appear to be able to produce brownish pigmentation. The Japanese plants often produce perianths and androecia (c.f., the plant collected by Hattori, June 1953, at Sakatani, Miyazaki, Japan); the nearctic phase appears to be uniformly sterile. This difference may prove to be purely nutritional. The female bracts of the Japanese plant are similar to leaves, but more longly ciliate-laciniate toothed. The perianth is obdeltoid or broadly obcuneate, with the dorsal and postical keels equal in length, neither of them winged or dentate; the truncate and wide mouth is copiously laciniate, with the laciniae running out in slender cilia. It is possible that a knowledge of the

reproductive features of the nearctic *ciliigera* might demonstrate the existence of marked differences in these, consequently warranting a specific separation between *P. japonica* and *ciliigera.* In the absence of reproductive structures in the latter this remains speculative, and can have no bearing on the status of this plant. Clearly, on the basis of vegetative characters, a specific separation of *ciliigera* from typical *P. japonica* is hard to maintain, and if subsp. *ciliigera* should be raised to the rank of an autonomous species, *P. ciliigera* (a course suggested as desirable by my Japanese colleagues), a separation would have to be based on geography as much as on morphology.

Segawa (1947) has just demonstrated that in the subsp. *japonica* the haploid chromosome number is 9, *i.e.,* 8 + X (♀) and 8 + Y (♂). This is exactly the condition in *P. asplenioides.*

Plagiochila japonica subsp. **ciliigera** subsp. n.

Fig. 34:1-7; 35-36

P. japonicae typicae similis; differt foliis caulis principis lingulatis vel parce ovato-lingulatis (1.9-2.1:1), lateribus paene parallelis, marginibus ventralibus minime convexis. Typus: Sylamore National Forest, Stone Co., Arkansas (*Anderson*).

In flat *pure green* patches over calcareous rocks. Shoots subsimple, occasionally with diffuse monopodial branching, with leaves *ca.* 3.5-3.8 to a maximum of 4.2 mm wide; plants a *pellucid pure green to pale green,* the stems often brownish, the entire plant *strongly nitid when dry.* Stems *ca.* 210-235 μ, occasionally 275-285 μ in diameter, 160-180 μ high, the cortex yellowish-brown, of narrow, strongly elongate cells (postically *ca.* 15-17 μ wide x 70-80 μ long, slightly thick-walled; antically 14-16 μ wide); cortex 2-3-stratose, of thick-walled cells, much narrower than cells of medulla (which are 20-30 μ in diameter); stems 12-14 cells high. Rhizoids virtually absent on leafy aerial shoots. Leaves slightly distant to contiguous, somewhat obliquely, usually characteristically *narrowly rectangular, not distinctly dilated near postical base, ca.* 810 μ wide x 1650 μ long (*2.1-2.2 × as long as wide*) to 900-975 μ wide x 1800-1850 μ long (*1.85-2.1 × as long as wide*), *on robust shoots narrowly rectangular and at times 2.2-2.6, exceptionally 3.0 as long as wide* (then 650-790-890 μ wide x 1900-1950 μ long); *postical leaf-margin nearly straight to slightly arched* and not or exceedingly weakly dilated at base, bearing 2-5 linear, spinose acicular teeth on the distal 0.4-0.7 of the margin, the *basal portion totally edentate;* postical base extremely short-decurrent to obsoletely decurrent, the basal 0.2-0.3 often narrowly, weakly reflexed; antical margin short-decurrent, nearly straight, usually subparallel for most of its length to postical margin, *the distal one-fourth to one-third with 0-2 relatively short, spinous, acicular teeth; leaf apex subtruncate to narrowly rounded,* usually terminated by two short lobes ending in acuminate, acicular teeth; leaf-margin, as a whole with 4-8 teeth;

teeth (except for the two apical) very narrow-based, *acicular, usually uniseriate to base, 4-5, occasionally 6 cells long* (those of antical margin often shorter), to 175-230 μ long, formed of narrow cells (15-22 μ wide) 2.2-3 × as long (42-45 up to 54-60 μ) as wide, issuing usually from a base formed by only two cells; leaves spreading horizontally, nearly flat, the antical base with cnemis vestigial, usually less than one-fourth the leaf-length, the long axis of the leaf at *ca.* 55-75° with

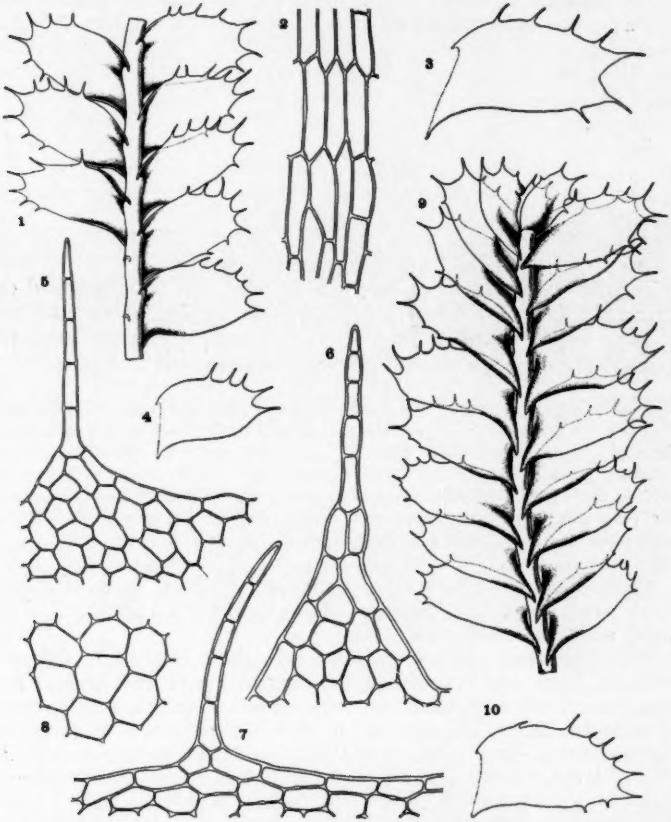

Fig. 35. *Plagiochila japonica* subsp. *ciliigera* Schuster. 1. Medium-sized shoot (x 10.2); 2. Cortical cells of postical face of stem (x 185); 3-4. Leaves (3, x 14; 4, x 9); 5. Cilium from postical leaf-margin (x 150); 6. Apical tooth of leaf (x 150); 7. Tooth from middle of postical leaf-margin (x 150); 8. Median cells (x 150); 9. Mature shoot (x 10.2); 10. Leaf (x 14). (All drawn from material from the type locality.)

stem. Cells *large and pellucid,* thin-walled to slightly thick-walled and with small to moderate (and obscurely bulging) trigones, usually lacking intermediate thickenings in non-marginal cells; apical and median cells virtually isodiametric, *varying from* 29-32 μ *wide x* 31-39 μ *long to* 27-34 μ (averaging 29-30 μ), polygonal to quadrangular; basal median cells somewhat elongate, 32-34 μ wide x 40-54 μ long, rectangular, not forming a vitta; *marginal cells of leaves in one, locally two rows strongly elongate,* forming a discrete border (even in distal portions of leaves), near middle of postical margin *ca.* 54-68 μ long (with extremes of 40 and 75 μ) x 18-24 μ wide; at postical base elongate in 3-4 rows, *ca.* 15-20 x 60-75 μ, slightly thick-walled, marginal row of cells with the inner tangential walls slightly but not saliently thick-walled, often irregularly so, the elongate bordering cells not strongly set off from inner cells. Oil-bodies (ten-month-old material) very finely segmented, the individual globules small (less than 0.8 μ), in 4-8 rows (on surface examination of oil-body); thus appearing finely granular-papillose and sub-opaque rather than segmented; oil-bodies 5-8 per median cell, *ca.* 3 x 8-12 (14) μ and sublinear, to ellipsoidal, 5-6 x 10-12 μ. Chloroplasts 2.5-3 μ. Underleaves largely vestigial, where discrete formed *usually of* 1-2 *linear cilia* (when two connate at base for 1-2 cells), 3-8 cells long and each segment tipped by a linear hyaline papilla, formed of elongate cells, 15-18 μ wide x 58-64 μ long (except at base, where less elongate). *Asexual reproduction absent.* Sexual reproduction unknown.

Type.—Big Sink Hole, Sylamore National Forest, Stone Co., Arkansas (*Anderson*): Duke herb.; type fragments widely distributed. *Cotypes.* Sylamore National Forest, Stone Co., Arkansas, edge of "Big Sink Hole"; on shaded limestone rocks, April 14, 1952, *R. L. McGregor* 5413 (cotypes, same data, but Nos. 5414, 5415). McGregor was the first, apparently, to collect this taxon. The Anderson specimens have been designated as the type since they are much more abundant, giving a clearer idea of the species.

Otherwise known only from Blanchard Springs, north of Allison, Ozark Mts., Stone Co. Arkansas (*Anderson* 11702, 11704,-11706 p.p. mixed with *Lophocolea bidentata*).

This distinctive taxon resembles a very shiny form of *P. diffusa* or *floridana* (with which it shares the narrow leaves and general leaf-form, the very short postical leaf-decurrence). Furthermore, the leaves are distant to barely approximate as in *P. diffusa,* which it approaches (but scarcely equals) in size. From both of these species *P. japonica ciliigera* differs in the shiny cuticle, and particularly in the narrow-based aciculate marginal teeth of the leaves, which are only 1-3 cells wide at base, and end in a filiform row of narrow, elongate, cells formed of 3-5, rarely 6 superimposed cells. Nothing approaching the dentition of the leaves has been seen in either of these two species, although *P. sullivantii* occasionally shows similar marginal teeth. *P. japonica ciliigera* differs from the latter in several important regards, indicating only a distant relationship: (1) absence of any tendency for brownish pigmentation of the leaves; (2) much narrower, rectan-

gular leaves; (3) total lack of caducous leaves; (4) larger, more pellucid, cells.

The plants, though with thin and very delicate leaves, have them uniformly persistent. In the persistent leaves, the species differs at once from the *P. sullivantii-austini* complex (although the leaf-form may approach that of the latter species). No trace of leafy propagula was evident. Neither was any trace of sex organs found, leaving the reproductive mode of the species a matter of conjecture.

In the form and size of the leaf cells, *P. japonica ciliigera* is identical with *P. echinata,* but stands isolated among our other nearctic species. The cells approach the *"contigens"* type (of Carl) in that they are large (apical 27-34 μ and averaging isodiametric), possess thin walls without intermediate thickenings, and have small to slightly bulging trigones. The marginal cells in 1-2 rows may have the longitudinal walls (parallel to the leaf-margin) slightly to irregularly thick-walled; in this it approaches *P. diffusa,* in which this characteristic is, however, much more fully developed.

This taxon also agrees with *P. diffusa* in the strongly elongate form of the marginal cells (both of postical margin, postical base, and to a slightly less extreme degree, of the antical margin). In *P. japonica ciliigera* the development of the border of elongate marginal cells is, however, more strongly developed than in *P. diffusa* (or in any other nearctic species). Along the middle of the postical margin the cells average 54-68 μ long (with extremes of 40 to 75 μ) and are only 18-24 μ wide, *e.g.,* 2.5-3 ×, occasionally 3.5 × as long as wide. In *P. diffusa* we find the marginal cells only averaging 28-35, occasionally 40 μ long x 15-16, occasionally 17 μ wide. *P. japonica ciliigera* also is characterized by the strongly elongate 3-4 rows of cells at the postical base, formed of cells averaging 15-20 μ wide x 60-75 μ long (averaging *ca.* 3.6-4 × as long as wide, somewhat evenly thick-walled). This taxon lacks all trace of a vitta. The median cells, like the interior apical cells, are isodiametric (and little or no larger in size), but towards the base the cells become gradually slightly more elongate and short-rectangular (averaging 32-34 μ wide x 40-54 μ long, *i.e.,* considerably less than twice as long as wide).

In the dentition of the leaves, *P. japonica ciliigera* closely approaches the neotropical species of the Section Subplanae (Carl, 1931, p. 45, 76); the distal and postical leaf-margins are remotely ciliate. The cilia in the present species are generally based on 2-3 cells (Fig. 35:5, 7), and are uniseriate and formed of 4-5, occasionally 6 cells. These cilia are straight to slightly arched, stiff and slender (*ca.* 15-22 μ wide x 225 μ long); they are formed of cells 15-22 μ wide x 40-50 μ long, *i.e., ca.* 2.5-3 × as long as wide.

On juvenile leaves the apical cilia are occasionally sessile on distinct lobes, the leaf thus bearing two ill-defined acuminate apical lobes. In this, the juvenile leaves (which are often extremely narrow) approach those of *P. austini,* a species which is only remotely related to the present one.

Relationships.—The "patulate" leaves, with an undilated postical base, and narrow line of insertion, the remotely ciliate leaf-margins,

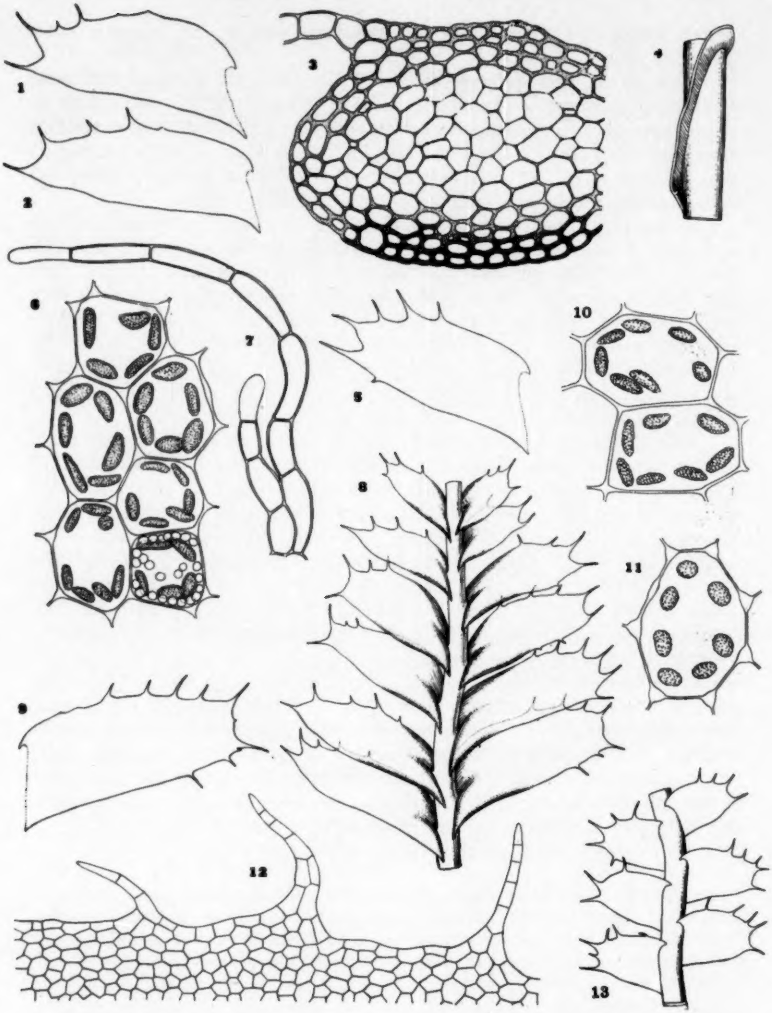

Fig. 36.—*Plagiochila japonica* subsp. *ciliigera* Schuster. 1-2. Leaves of the mod. *angustifolia* (x 16). 3. Stem cross-section, from robust plant (x 200); 4. Part of stem, lateral aspect, showing line of insertion of leaf (x 28); 5. Leaf (x 16); 6. Cells from above leaf-middle, with oil-bodies and in lower right-hand cell, chloroplasts (x 395); 7. Underleaf (x 250); 8. Shoot-apex of mod. *angustifolia* (x 13); 9. Leaf from plant of latter type (x 16); 10-11. Cells with

the laterally patent leaves, the pale green color, and the relatively large cells (of the *contigens* type), and the medium size of the plants all suggest *P. japonica* and its subspecies, *ciliigera,* belong to the Sectio Subplanae. As a member of this section, it is remotely related to such neotropical species as *P. amazonica* Spr., *P. kegeliana* St., *P. subplana* Ldbg., *P. hondurensis* Herzog, and *P. divaricata* Ldbg., species distributed from the Island of Dominica and Costa Rica to the Amazon basin.

Among neotropical species, a superficial similarity, if at best distant relationship, also appears to occur to *P. diffusa,* with which it agrees in (1) the narrow rectangular leaves, with a narrow line of insertion; (2) the discrete border of elongate marginal cells; (3) segmented oil-bodies; (4) distant to approximate leaves that spread laterally in a nearly flat plane, with the longitudinal axis of the leaf at an angle of 55-60° with the stem; (5) absence of a vitta. The larger cells, both of leaf-apex and leaf-margins, the peculiar aciculate cilia of the leaf-margins, the pale color, shining cuticle (when dry), and the slight development of thick tangential cell-walls of the marginal cells, as well as the form of the oil-bodies, all serve to separate *P. japonica ciliigera* from *P. diffusa.* In drying, a further very characteristic difference appears: *P. j. ciliigera* retains the flat orientation of the leaves; in *P. diffusa* they become deflexed and tubularly involute.

PLAGIOCHILA RHIZOPHORA Hattori

Fig. 36A, 36B

Plagiochila tridenticulata Hattori, Bull. Tokyo Sci. Mus. No. 11:65, 1944; Hattori, J. Hattori Bot. Lab. 8:22, 1952 (not of Taylor).

Plagiochila rhizophora Hattori, J. Jap. Bot. 25(7):141, fig. 57, 1950; Inoue, J. Hattori Bot. Lab. 20:63, fig. V, 1958.

Plagiochila otiana Hattori (in sched.; *nom. nud.*), and Hattori *in* K. Ochi, Shizen-to-Jinmon, 1:64, 1950 (*nom. nud.*).

Plants small, the stems to 2-5 (6) cm long, forming olive-brown to *brownish* patches, the *shoots nitid when dry.* Shoots 1.8-2.5 (3) mm wide; stems *ca.* 250-280 μ in diameter, sparingly branched, the branches all lateral and intercalary; postical stem face typically *rather freely rhizoid-bearing,* the rhizoids commonly extending towards apices of leafy shoots (only the weak mod. *parvifolia* occasionally almost rhizoid-free). Leaves obliquely spreading, distant or subcontiguous to contiguous, occasionally moderately imbricate, little convex to moderately convex, when flattened ovate-oblong, to 2.0 (2.5) mm long x 1.1 (1.5) mm wide (averaging *1.45-1.85 × as long as broad*); *antical margin strongly decurrent at base,* moderately to conspicuously

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oil-bodies, in 11 of the most pachydermous extreme seen (10, x 325; 11, x 450); 12. Cells of postical margin of leaf, with relatively weakly developed cilia (x 85); 13. Juvenile shoot-sector, postical aspect (x 16). (Figs. 1-9 from cotype, *McGregor,* Arkansas; 10-13, from *Anderson* 303, 1953, type.)

reflexed, *without teeth,* nearly straight to weakly convexly arched. Postical base *very short decurrent,* the stem extensively exposed in postical aspect; *leaf-apex commonly conspicuously bidentate to bilobed for 0.15-0.25 the leaf-length,* the teeth triangular and broad, often decurved, sharply acute to short-acumuniate, on *large leaves with commonly 1-2 (3-4) accessory smaller teeth,* near the apex and on distal half of postical base, of which one is sometimes elaborated as an incipient lobe, the *leaf then subequally tridentate to trilobed at apex;* posterior margin arched, often strongly so, edentate below but with 1-3 teeth in the distal one-third to one-half. Marginal cells 17-20 x 17-25 μ; *median cells 25-29 x 30-34* μ and with coarse and often bulging trigones; basal cells 17-22 x 38-50 μ, or larger, with coarse, nodulose trigones; cuticle smooth. Oil-bodies 5-8 per cell, 3 x 4-7 μ up to 4 x 4-7 μ formed of rather coarse, distinct, globular segments (usually 9-16 segments visible in surface view per oil-body). *Underleaves vestigial.* Leaves persistent, without propagula; *asexual reproduction evidently absent.*

Dioecious. Gynoecia terminal on leading stems, *with* 1 (-2-3) *innovations.* Perichaetical bracts little larger than stem leaves but more strongly dentate, the antical margins more strongly decurved, the ventral margin strongly arched and dilated, coarsely paucidentate. Perianth in lateral aspect campanulate, with rounded, bilabiate mouth bearing 20-24 spinulose teeth on each "lip"; teeth subequal, rather small (1-5 cells long x 1, occasionally 2 cells broad basally) but dense; dorsal and postical keels subequal, *unwinged.*

Type.—Kadoishihara, Sumino, Nii Distr., Ehime Pref., Prov. Iyo, Japan (*K. Oti* 805, 1944!); type in herb. Tokyo Sci. Mus., and in herb. Hattori; duplicate in herb. of author.

Distribution.—The typical species (subsp. *rhizophora*) appears restricted to Japan. The species was reported as *P. tridenticulata* from southern Kiushiu by Hattori (1944) and from the same area, under the same name, by Hattori (1952). Dr. Hattori (in litt.) states that his report was based on poorly preserved plants, in the herb. Tokyo University. He now considers the Kiushiu plant as a "depauperate plant of *P. rhizophora,*" a species based on Shikokian material. Inoue (1958, p. 65) also treats these plants under *P. rhizophora.* Typical *P. rhizophora* thus appears to be restricted to Kiushiu and Shikoku, Japan. I have seen the following specimens:

JAPAN: Kadoishihara, Sumino, Ehime Pref., Prov. Iyo (*K. Oti* 805, *type!*); Mt. Ichifusa, Kumamoto Pref., on lower portion of tree trunk (*K. Mayebara* 1329!; a small, depauperate form with very few rhizoids!); Mt. Tenso, Tokyo Pref., on bark (*Hattori* 3756!; a relatively dense-leaved and robust phase, with the leaves relatively strongly bilobed, with short-acuminate or acute lobes that are often deflexed); Mt. Ishizuchi, Ehime Pref. (*S. Hattori* 3058!; a small form, often with few rhizoids, with remote to contiguous leaves; approaching most closely to the Alaskan plant!).

In addition to the restricted distribution in Japan, atypical plants referable to *P. rhizophora* have been collected in the Aleutian Islands, Alaska, and reported (Clark and Frye, 1948, 1949) as *P. tridenticulata;* these plants are sufficiently different so that I prefer to consider them as subspecifically distinct.

Ecology.—The Alaskan (Aleutian) plant is found on tundra; the Japanese populations commonly on the bark of trees, associated at times with *Herberta sakuraii* subsp. *sakuraii* in a form exceedingly similar to subsp. *tenuis* (in *Hattori* 3058). In Japan occurring both on the trunk and on its lower portions, often mixed with various Lejeuneae and *Radula,* and on humus, or soil-covered rocks.

Variation and Differentiation.—The very few collections of this plant give only a limited idea of its variability. The often abundant rhizoids, obsolete only on weak plants, the shiny texture, as well as the antically long-decurrent leaves, with the dorsal margin more or less reflexed (at least on mature leaves) and the often relatively broad leaves averaging less than 1.8× as long as broad, distinguish the plant from *P. tridenticulata,* with which it has been confused.

The Japanese plants "tend" to develop some obovate to obovate-obcuneate leaves, and evidently never show a "tendency" for the leaves to be ampliate above the postical base. Also, the lobes and teeth are relatively broad-based rather than aciculate; the teeth of the leaves are always very few in number. (These features are clearly shown in Inoue, 1958, fig. IV). In all of these features, as well as in the ability to develop rhizoids in some abundance, the Japanese plants differ from the American ones, which are described below. There is also a marked "tendency" in the Japanese plants for the development of coarser trigones, particularly of the basal cells. However, one of the Japanese plants (*Hattori* 3058) approaches the Alaskan plants rather closely in having less coarse trigones and very few rhizoids. Indeed, if it were not for the latter plants, I would have serious reservations about considering the Japanese plants and the Alaskan ones conspecific. For example, the imbricate-leaved, broad-leaved, deeply bilobed leaved plants of *Hattori* 3756, which are copiously rhizoidous, have a very different aspect than the American plants. Evidently a variable and polymorphic series is at hand. Hattori (in litt., Dec. 1, 1957) also believes that the Alaskan plant is "closely related to Japanese *P. rhizophora,*" and Inoue (in litt.) has determined the Alaskan material as *P. rhizophora.*

Apparently allied to the Alaskan plant is one from British Columbia, sent to me as *P. rhizophora* by Dr. H. Persson, the collector. This plant, with more copious dentition, retains the large cell-size, and the tendency towards elaboration of two apical teeth as incipient lobes (Fig. 36B). In other respects, the plant is very different, and it probably does not represent a mere modification of *P. rhizophora.* Indeed, with its inclusion within *P. rhizophora,* the latter acquires a distressing polymorphism. Considering the limited materials available, it probably will prove best to separate the material of the species into three phases as follows:

1. **Leaves tending to be widest above the middle, typically with 2-3 teeth elaborated distally as incipient lobes, otherwise edentate (or with merely 1-2 [3-4] accessory, smaller teeth); the teeth broad-based, never sharply spinose; mature plants freely developing rhizoids; mature plants with leaves long-decurrent antically. Japan............*P. rhizophora* subsp. *rhizophora***
1. **Leaves oblong-ovate to ovate, never (or only abnormally) widest above the middle, typically with 2 incipient lobes and 1-several accessory teeth, the teeth often spinose; plants with rhizoids always rare or virtually absent; mature leaves moderately decurrent antically. N.W. Pacific ....*P. rhizophora* subsp. *confusa* 2**
2. **Leaves strongly ovate, mostly 1.25-1.45x as long as broad, the postical leaf-margin with usually 6-12 irregular, spinous teeth extending down to within 0.2 of the leaf-base; median cells averaging (30) 32-35 μ wide; plants robust, 2.4-3.5 mm wide, occasionally terminally branching. British Columbia. .... *P. rhizophora* subsp. *confusa* (*typical*)**
2. **Leaves ovate-rectangulate, 1.5-1.8x as long as broad, the postical leaf-margin with 0-2 (3) accessory teeth restricted to distal half of leaf; median cells averaging 25-27 μ wide; plants small, 1.8-2 mm wide. Alaskan. .... *P. rhizophora* subsp. *confusa* (mod. *angustifolia-parvifolia*)**

Plagiochila rhizophora subsp. **confusa** subsp. n.
Figs. 36A:1-8, 36B

Mediocris, ± brunneola vel rufo-brunneus, cum foliis 1.8-2.4 (3) mm latus, parum ramosus; postice sine radicellosus. Folia caulina oblique patula, contigua, in plano ovata vel ovato-oblonga, ad 950-1050 μ longa, 600-625 μ lata, vel 1600-2000 μ longa, 1175-1660 μ lata, apice valde emarginato-bidentato vel tridentato, dentibus triangulatis, acuminatis vel acutis, saepe 1-2 dentibus multo minoribus adjectis; margine postico arcuato, superne bi- vel trispinuloso. Cellulae mediae (23) 25-27 (28-35) x 30-36 (30) μ, trigonis magnis vel minoribus. Amphigastria rudimentaria. Typus: Graham Island, Queen Charlotte Islands, British Columbia (*H. Persson,* July 25, 1957).

Plants in low patches, *small, brown, nitid when dry,* forming intricate patches. Shoots 1.8-2.5 (3-3.5) mm wide x 8-12 (16-25) mm long, the aerial shoots unbranched or occasionally with a *lateral, leafy intercalary branch that is geniculate just above its origin,* sporadically (in type) with furcate terminal branching; intercalary branch bearing at the geniculation 1 or 2 rhizoidous stolons, that are positively geotropic and possess only vestigial leaves. Stems brownish, firm, 190-225 (300) μ in diameter; dorsal cortical cells *ca.* 18-22 μ wide x 50-60 (68) μ long, yellowish but only moderately thick-walled. *Rhizoids absent,* except near origin of branches. Leaves *subcontiguous to weakly imbricate,* on weak stems often remote, short-decurrent postically, moderately decurrent antically, laterally patent at an angle of *ca.* (45) 50-60°, *both when dry and when moist,* postically concave-canaliculate owing to the fact that both antical and postical margins are at least weakly deflexed in the distal halves of the leaves; leaves

basically *oblong-ovate in shape, on robust plants often strongly ovate, on weak shoots often merely oblong,* ranging from *ca.* 500-525 μ wide x 900-950 μ long to 525-550 μ wide x 850 μ long up to 600-625 μ wide x 950-1050 μ long (*length averaging from 1.5-1.8X the maximal width*) in weak (Alaskan) phases; in robust phases from 1175-1275 μ wide x 1700-1750 μ long to 1360 μ wide x 1600 μ long up to 1600-1660 μ wide x 2000 μ long (type); *leaf widest usually a little above base,* but sometimes at or near the leaf-middle; postical leaf-margin moderately strongly arched, *weakly to strongly dilated above postical base,* the leaves on mature shoots *widest in the basal one-third,* the postical and antical margins gently convergent in distal 0.5-0.65 of the leaf; antical margin nearly straight to *more often weakly convex,* in the basal half weakly deflexed and thus with only a slightly developed cnemis. *Dentition very sparse* on weak plants but *robust plants copiously spinose-dentate,* the leaf-apex with *usually two teeth elaborated as incipient lobes* (these acute to subacuminate from a triangular base), the teeth separated usually by a lunate sinus rarely interrupted by a small accessory tooth; *postical margin with (0) 1-2 (3) spinose teeth on weak plants,* on robust plants *with up to 7-11 sharp teeth,* the teeth when well developed *slender, almost aciculate and formed of (2) 3-4 superimposed single cells,* inserted on a base 2-5 cells wide. Cells of teeth *ca.* 24-42 μ long x 15-20 μ wide, locally up to 3-3.5× as long as broad, the terminal cells of the teeth occasionally sublinear and 15 x 55 to 16-18 x 62 μ (then 3.5-4.5× as long as broad). Antical leaf-margin usually totally edentate, *the leaf as a whole thus with (2) 3-5 sharp teeth* (weak plants) *up to 12-18 teeth* (robust plants). *Cells large and pellucid,* the subapical usually (22) 25-28 (30) μ wide x (24) 30-33 μ long, the median *ca.* (23) 25-27 (28-30) μ wide x (27) 30-36 (40) μ long (weak forms) up to (30) 32-35 μ wide x 33-40 (42) μ long (type; robust plants) the basal cells along leaf-midline *ca.* (20) 21-24 x 40-50 (60) μ (weak forms), up to (24) 26-30 x (36) 40-55 (60) μ (robust plants; type); cuticle smooth; trigones everywhere distinct, often sharply defined and distinctly nodulose; intermediate thickenings absent, except along longitudinal walls of isolated, longer basal and subbasal ± thick-walled cells. Oil-bodies finely granular-segmented, *ca.* 5-10 per cell. Underleaves vestigial, difficult to demonstrate, of a median cilium 5-6 cells long ending in a slime papilla (formed of a narrow cell up to 10-12 x 42 μ), associated with 1-2 basal, short cilia, formed of shorter cells, which are connate with the leading cilium at the very base. *Asexual reproduction absent.*

Type.—CANADA, BRITISH COLUMBIA: Queen Charlotte Islands, Graham Island, Dawson Inlet, along a brook with *Hypnum dieckii* (*H. Persson,* July 25, 1957). The type material is in the collection of the Riksmuseum, Stockholm, Sweden; a portion of the type is in the author's herbarium.

Distribution.—Known only from the Aleutian Islands, and from southeastern coastal Alaska, south to British Columbia. In addition

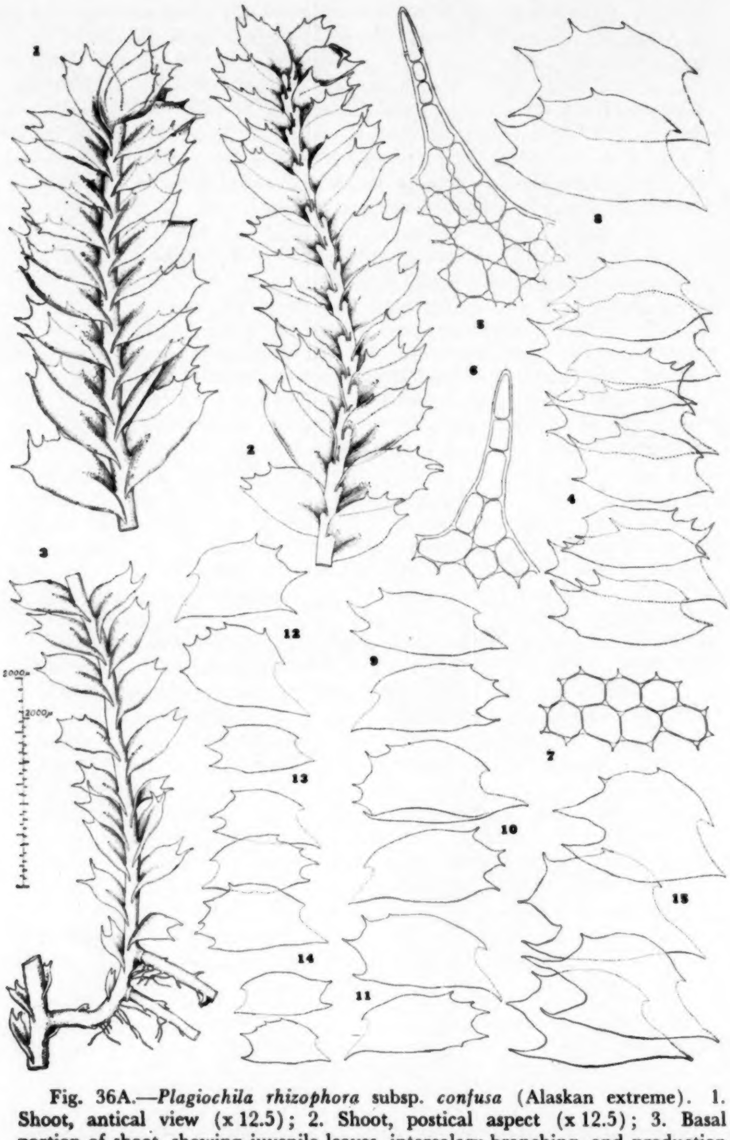

Fig. 36A.—*Plagiochila rhizophora* subsp. *confusa* (Alaskan extreme). 1. Shoot, antical view (x 12.5); 2. Shoot, postical aspect (x 12.5); 3. Basal portion of shoot, showing juvenile leaves, intercalary branching, and production of stolons (x 12.5); 4. Eight leaves, showing range in variation (x 15.5); 5-6.

to the type, I have seen a few plants of the species from ALASKA: Port Alice (*Frye* 728! on wet rocks, admixed with ***Plagiochila satoi, Metzgeria hamata*** and ***Riccardia multifida;*** the identity of these plants with ***P. rhizophora s. lat.*** has been confirmed by Mr. H. Inoue); on tundra, near sea-level, Peaceful Valley in the vicinity of Massacre Bay, Attu Island, Aleutian Islands, (***Margaret Bell Howard*** 836, Nov. 15, 1945); reported by Clark and Frye (1948, p. 254) as *"Plagiochila tridenticulata."* Presumably the other collection (*Howard* 541) from Attu Island, cited by Clark and Frye (*loc. cit.*) as ***P. tridenticulata,*** as well as plants reported under the latter name, from Adak Island, Aleutian Islands (Clark and Frye, 1949, p. 60) belong to this taxon. The Alaskan plants all represent a mod. *parvifolia-paucidentata-angustifolia*. The single collection from British Columbia (type) is of a plant habitually dissimilar, more robust, with broader, more ovate leaves.

The plant from British Columbia occurred along a brook "with *Hypnum dieckii.*" The locality is on the west coast of Graham Island, and only a "mile from the single locality for a Hymenophyllaceae on the Pacific Coast, the Japanese *Mecodium wrightii.*"

Differentiation.—Mature shoots of ***P. rhizophora*** subsp. *confusa* are more apt to be confused with ***P. echinata*** than with ***P. r. rhizophora;*** the separation from ***P. echinata*** is discussed below. Such mature shoots of the American phase of ***P. rhizophora*** differ from mature plants of the Japanese, typical subspecies as follows: (a) the leaves are clearly ovate, and widest a little above the postical base; this is foreshadowed even on many leaves of the narrow-leaved mod. *parvifolia-angustifolia* from the Aleutian Islands; (b) the dentition of the leaves is much more copious, the teeth are narrower-based and more nearly ciliiform, although hardly as strongly so as in ***P. echinata;*** (c) the oil-bodies, judging from the dry plants from British Columbia, are oval to ellipsoidal and finely granular, exactly as in ***P. echinata;*** (d) the shoots are virtually without rhizoids, except near the origin of branches, even on robust and mature shoots. These differences, collectively, suggest that ***P. rhizophora*** subsp. *confusa* may have to be elevated to the status of a discrete species. I have not done this because the Alaskan plants, all of which belong to a mod. *angustifolia-*

Cells and teeth of middle of postical leaf-margin (x 180); 7. Median cells (x 180); 8. Two rather juvenile leaves, of the larger phase from British Columbia (portrayed in Fig. 36B) (x 15.5). *Plagiochila rhizophora* subsp. *rhizophora*. 9-11. Six leaves, from type material (x 15.5); 12. Two leaves (x 15.5); 13-14. Six leaves of a small-leaved extreme (x 15.5); 15. Four leaves, of a broad-leaved extreme (x 15.5). (Figs. 1-3 drawn to one scale, the scale to the right [lower left-hand of figure]; figs. 4, 8-15 drawn to the adjoining scale immediately to the left). (Figs. 1-4, 6-7, from the plant collected on Attu Island, Alaska, *Howard;* 5, 8, from the type, collected on Queen Charlotte I., *Persson;* 9-11, from the type of subsp. *rhizophora, Ochi* 805, also illustrated in Inoue, 1958, fig. IV; 12, from *Mayebara* 1329; 13-14 from *Hattori* 3058; 15, from *Hattori* 3756.)

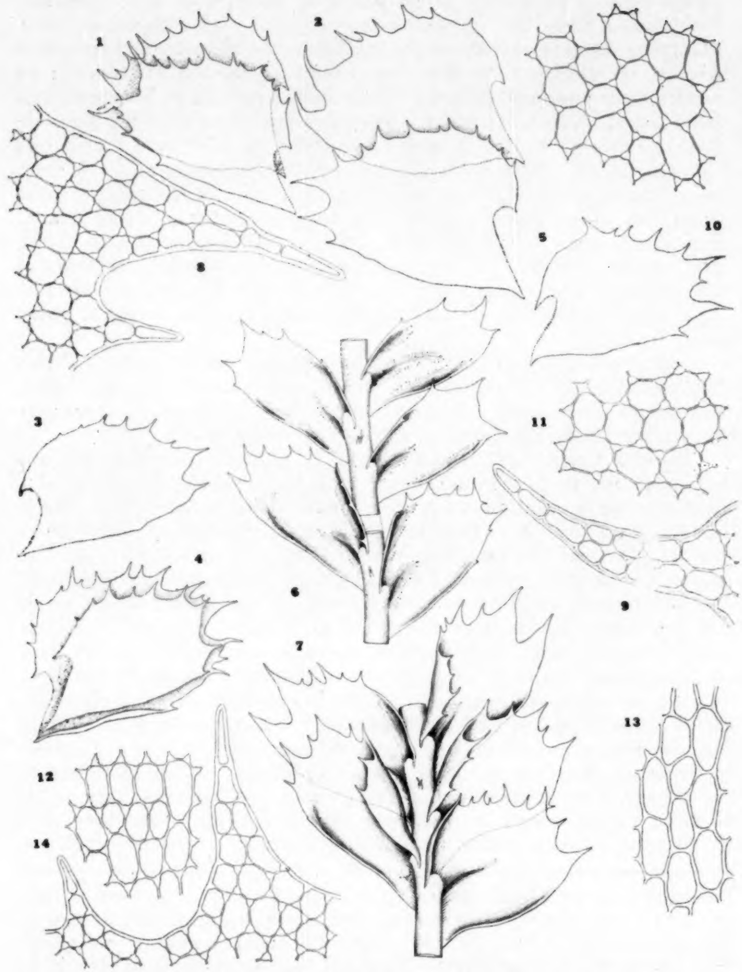

Fig. 36B.—*Plagiochila rhizophora* subsp. *confusa*. 1-5. Leaves, showing variation in size and dentition (x 13.5); 6-7. Shoot-sectors, postical view, of respectively lax- and dense-leaved shoots (x 13.5); 8-9. Cells from leaf-apices, each showing an apical lobe-like tooth (x 165); 10-11. Median cells (x 165); 12-13. Basal cells, along the leaf-midline (x 165); 14. Cells from along the postical leaf-margin, showing optimal development of dentition (x 165). (Figures all drawn from the type specimen, from Queen Charlotte I., British Columbia.)

parvifolia approach the type material of *P. rhizophora rhizophora,* particularly in the paucidentate, 2-3-lobed leaf apices and in the narrow, virtually oblong leaves. Such Alaskan plants are separable from subspecies *rhizophora* as follows: (a) leaves narrower usually, occasionally fully twice as long as broad, lingulate-ovate to oblong-ovate but tending to be slightly dilated above the postical leaf-base; (b) teeth of the leaves often more aciculate, reminiscent of those of small forms of *P. japonica;* (c) rhizoids virtually absent, except near origins of leafy branches; (d) cells usually with trigones much less marked, but the cell-size tending to be slightly greater; (e) apical, incipient leaf-lobes usually shorter, separated by a shallower and often narrower sinus. These differences are all quantitative, and may not all prove genetic in origin. However, the variability of *P. rhizophora* is such, when the mod. *parvifolia* (*Mayebara* 1329) is compared with the type (*Oti* 805) and that in turn compared with the robust mod. *megafolia-densifolia-latifolia-fissifolia* (*Hattori* 3058), it seems impossible to regard the Alaskan plants as a mere modification. In both the mod. *parvifolia* of subspecies *rhizophora,* and in "normal" or small plants of subspecies *confusa,* there is a high incidence of plants with bilobed leaves. This evidently led Clark and Frye and Hattori to confuse the taxon with *P. tridenticulata,* which also has largely coarsely bidentate to shallowly bilobed leaves and is hardly smaller in size. However, the Alaskan collection cited above, determined by Clark as *P. tridenticulata,* shows a number of more nearly mature shoots, in which the leaves (Fig. 36A: 1-4) are ovate to ovate-lingulate and possess the characteristic tendency for the leaf-apices to have two of the teeth elaborated as incipient lobes. The teeth of the more nearly mature leaves are also characteristically ciliiform, thus exhibiting a similarity to species of the Sectios Subplanae and Acanthophyllae of Carl (1931). Equally suggestive of these sections (and equally separating the plants from the Bidentes, to which *P. tridenticulata* belongs) are the large and relatively delicate leaf-cells and the persistent leaves. The underleaves are quite vestigial. The strongly shining color, when dry, at once separates the plants from *P. tridenticulata,* and is suggestive of the Subplanae. The presence of few and segmented oil-bodies is an added feature separating *P. rhizophora* from the Sectio Bidentes (and, therefore, from *P. tridenticulata*).

The sparse and poorly developed Alaskan material can be referred to *P. rhizophora* only with considerable reservations; it, however, cannot be placed elsewhere, and is surely not mature enough to warrant its segregation into a separate species. With the discovery of more mature plants, and the study of the limits of variability of the American populations, it may prove necesary to segregate the material as a distinct species. For the time being the present disposition appears to be the only rational one. The plant might also be confused with a mod. *parvifolia* of *P. japonica.* However, I have not seen any plants of any form of *P. japonica* in which the juvenile stems bear similarly bilobed leaves, whose shape is reminiscent of those of *P. tridenticulata.* On the other

hand, the leaf-cells very closely match those of *P. japonica* in size (see Hattori, 1944, p. 54). *P. japonica* sometimes shows an identical tendency to elaborate two of the apical teeth into incipient lobes; there is also a tendency to have the teeth of the postical margin few in number (2-4 usually) and often restricted to the distal 0.4-0.5 of the postical margin (see Hattori, *loc. cit.*, fig. 30). The cilia of the leaves may be remarkably similar (compare Hattori, *loc. cit.* fig. 30d), and very similar trigones may be developed in typical *P. japonica*. The leaf-shape of well-developed leaves of *P. rhizophora* subsp. *confusa* closely approximates the leaf-shape of the Japanese plant cited as *P. sciophila* by Carl (1931, fig. 10e); the latter is considered to be a synonym of *P. japonica* by Hattori (1952).

I have studied a long series of Japanese specimens of *P. japonica* in the unrealized hope of discovering juvenile stems which match those of the Alaskan plant here referred to subsp. *confusa*. Although the juvenile leaves may show a similar incipient bilobing, and may be equally sparingly ciliate on the distal portions of the postical margins, the leaves of such juvenile plants always appear narrower than in the Alaskan plant, and the teeth of the leaves are definitely more sharply aciculate. As a consequence it appears impossible to refer the present plants to *P. japonica*.

The more or less juvenile Alaskan plants exhibit some superficial similarities to *P. austini*, enhanced by the brownish color, nitid texture, the high incidence of shallowly bilobed leaves, and the size. The cells, however, are larger than in *P. austini* and the leaves appear to be uniformly persistent (they are much broken in the fragmentary and poorly preserved specimen I have seen, but definitely give the impression of being non-caducous). The more nearly mature leaves, also, are slightly more decurrent antically and are narrowly but unmistakably ovate to ovate-lingulate in shape; they bear, in part, more aciculate teeth. The latter are reminiscent of those of *P. sullivantii*, a species with pluriciliate juvenile leaves of very different aspect than the bidentate to bilobed juvenile leaves of the present taxon. I do not believe that any real affinity to the Choachinae (the section to which I refer *P. austini* and *P. sullivantii*) exists; the basically ovate leaf-shape argues against such a relationship, as do the persistent leaves.

The most salient features of the present plants thus are: (1) the shiny texture when dry; (2) a brown to yellow-brown, warm pigmentation; (3) ovate to ovate-lingulate leaves, with (4) the leaf-apices always showing a more or less discrete tendency for the elaboration of two teeth to form incipient lobes; (5) the other teeth few, confined to the distal half of the postical margin on weak plants (on robust plants more copious), slender and spinose and formed at least at the apex of elongated cells; (6) underleaves vestigial; (7) leaves contiguous, laterally patent, evidently persistent; (8) relatively large leaf-cells. The leaf-cells varied widely in the several plants seen. On some juvenile leaves they averaged only 24-25 μ wide in the leaf-middle; on mature leaves they ranged to 28-30 μ wide or more, at least under "favorable" conditions. Presumably, the maximal cell-size is attained only under nearly optimal environmental conditions. Judging from the thoroughly juvenile aspect of the Alaskan collections seen, the plants must have grown under difficult conditions, hence the maximal potential cell-size to be expected was not realized. The more robust

plants from the Queen Charlotte Islands had much larger cells.

The tendency for the leaves to show incipient bilobing, the ovate leaf-shape of the robust shoots, the shiny texture, the rather delicate and large leaf-cells, and the development of only a few slender and nearly ciliiform marginal teeth of the leaves are clearly suggestive of the Appalachian *P. echinata.* The much narrower leaves and less copiously developed dentition easily serve to separate weak forms of the two species. I have never seen narrow, rectangulate, bilobed juvenile leaves that are reminiscent of mature leaves of *P. tridenticulata* in *P. echinata.* The resemblance between *P. rhizophora confusa* and *P. echinata* is further increased by the sporadic presence of terminal branches, in both species, at least on mature, well-developed material.

The affinity to *P. echinata* is most sharply indicated in the plants from British Columbia which appear to represent the mature phase of the American subspecies, and indicate that *P. rhizophora* subsp. *confusa* may deserve treatment as a full species. In these plants the leaves are clearly ovate, with the maximal width at about one-third the distance from the leaf-base; the incipient lobes of the leaf-apex are accompanied by a series of sharp, irregular, shortly acuminate teeth that extend from apex virtually to the postical leaf base. The leaf-shape, the incipient bilobing of the leaf-apex, the distinctly collenchymatous cells, shiny cuticle, and the finely granular-segmented oil-bodies (which were still distinct in a few cells of the dried plants) are closely reminiscent of *P. echinata.* However, the teeth of the leaves are much less slenderly spinose and never ciliiform as in *P. echinata.* Weak and juvenile phases of *P. echinata* (Fig. 33:3-7) may have similar dentition, with the teeth hardly ciliiform. This does not serve to invalidate the distinction maintained between the two taxa, since juvenile *P. rhizophora confusa* approaches *P. tridenticulata,* juvenile *P. echinata* approaches mature *P. r. confusa,* while mature *P. echinata* is a much more elaborately ciliate-leaved plant than any phase of *P. rhizophora.* In some respects, the ovate-leaved *P. rhizophora confusa* is almost intermediate between the often oblong-obovate-leaved *P. rhizophora rhizophora* and *P. echinata.*

A certain superficial similarity exists between the plants of the present taxon and weak shoots of *P. fruticosa* Mitt., a Japanese species. Both may have similarly formed leaves, tending to show incipient bilobing apically, and with only a few accessory teeth. *P. fruticosa,* however, has much smaller cells (16-20 μ wide), with equally thickened walls; it has less spinose-ciliate dentition, free, furcate, terminal branching, and slightly more suberect leaves. The two taxa are surely only distantly allied.

A much closer affinity surely exists to *P. rigidula* Hattori et Inoue (*in* Inoue, 1958, p. 61, fig. III). However, this species is based on large plants (3-4 mm wide), which possess paucidentate leaves that very closely suggest those of some forms of typical *P. rhizophora,* especially in the tendency for the leaf to become slightly oblong-obovate. The plant is also described as with remote leaves that are conspicuously long-decurrent dorsally. Inoue (in litt.,

to whom part of the type material of subsp. *confusa* was sent in 1957, under this manuscript name) stated that a distinct taxon was at hand. The large cell-size of subsp. *confusa,* on the larger plants (2.4-3.5 mm wide), averaging 32-35 μ wide in the leaf-middle, appears to preclude any identity with *P. rigidula;* Inoue (1958, p. 61) states that the cells of the latter are only "about 24 x 26 μ." Nevertheless, the two taxa must be closely allied, as is evident from a comparison of weak shoots of *P. rhizophora* subsp. *confusa* (Fig. 36B:6) with *P. rigidula* (Inoue, *loc. cit.,* fig. III:2). Note, particularly, the extreme similarity in leaf form.

Sectio VI. YOKOGURENSES Inoue

Plants similar in most respects to those of the Contiguae, differing from them primarily in (a) the more or less shiny color; (b) the fragmentation of the distal half of the leaf, which drops off irregularly as large plates or lobes, or more often as a unit; (c) occasional development of distinctly lamellate underleaves.

Plants, when well-developed, ascending and *rather freely pseudo-dichotomously furcate* (branching *via* terminal branching) from a rhizomatous base, but on weak plants with only a few monopodial, intercalary branches, the aerial shoots then simple or nearly so. Plants light green, translucent, mostly 2.5-4 mm wide. Stems brownish, the cortex of (2) 3-4 strata of thick-walled cells. Rhizoids few or absent on aerial shoots. *Leaves laterally patent,* not postically secund, *weakly imbricate to distinctly imbricate,* rarely so strongly imbricate that the ampliate postical leaf-bases become contiguous and hide the stem in postical aspect, *strongly ovate-falcate, the postical bases prominently dilated, but short-decurrent;* decurrent strip and margin immediately above often loosely reflexed, but *without formation of a sharp crista or water-sac;* antical margin strongly deflexed in at least the basal two-thirds, concavely arched; postical margin above dilated base nearly straight, spreading at an angle of 95-110° usually, armed with usually 2-5 (7) spinose, but rather small teeth; apex somewhat narrowed through gradual and nearly uniform convergence of postical and antical margins, armed with 2-4 rather strong, spinose teeth; the adjoining distal end of the antical margin often with 1-2 small teeth. *Underleaves small, usually formed of a small lamella* bearing short teeth ending in slime papillae, on robust plants occasionally larger, bifid to strongly ciliate. Cells medium-sized, of the "*hypnoides*" type, averaging (17) 20-25 μ wide medially, with rather finely *segmented-appearing oil-bodies;* cells with small to somewhat bulging trigones; *without a basal vitta;* oil-bodies segmented-papillose. *Asexual* reproduction *via* fragmentation of the leaves, the distal half or more of the leaf dropping free (often shortly after reaching maturity), the *mature plants thus commonly with only truncate, irregular leaf-stubs,* except at tips of branches; the caducous leaf-sectors producing propagula, from which new plants develop.

Androecia intercalary, the bracts in 4-7 pairs; bracts diandrous.

Gynoecia terminal on leading branches, with 2 innovations (or sometimes with single innovations; then becoming pseudolateral). Perianth urceolate and irregularly toothed at the wide mouth. Archegonia about 15.

Including only the sole regional species, *P. yokogurensis fragilifolia.* The sectio is very close to the Contiguae, in the ovate-falcate leaves with rather long-decurrent dorsal, but short-decurrent postical bases, in the form and number of the marginal teeth, and in the form, size and number of the oil-bodies. Differing from sectio Contiguae, however, in (1) the copious, pseudodichotomous branching; (2) the excessively fragile leaves, which, as they approach maturity, usually break irregularly in half, the distal half being caducous and developing (either shortly before or shortly after breaking free) leafy propagula. Possibly, when better known, this species may be included as an aberrant member of the Contiguae.

This section appears to be Asiatic-Appalachian in distribution. *P. yokogurensis* is the only American species presently assignable to it.

A distant affinity of the Sectio Yokogurenses may occur with the plants I assign to the Sectio Cristatae, sectio nova. The type of this section is *P. cristata* (Schwartz) Dumort., Rec. d'Obs., p. 15, 1835. This plant (and the section) agree with the Yokogurenses in several important respects: (a) The leaves ampliate, particularly with the strongly dilated and arched postical base, which extends wholly across the stem, showing a close similarity to the luxuriant extremes of typical Japanese *P. yokogurensis* (compare Carl, 1931, fig. 9E with my Fig. 40:2); (b) the narrowed distal portions of the leaves widely spreading (85-110°), attenuated and drawn out; (c) the mode of dentition; (d) the short decurrent postical, but long-decurrent antical leaf-bases; (e) a tendency, weak on most phases of *P. yokogurensis,* but according to Carl marked in *P. cristata,* for crista-formation; (f) reproduction by caducous leaves. In the latter respect, there are both similarities and differences between the Yokogurenses and the Cristatae: the former have the leaves distally caducous, with remnants of the leaf-bases retained; the latter, judging from the figure in Lindenberg (Spec. Hep. Fasc. 1: pl. 6, figs. 1, 5, 1840) have the leaves caducous at the very base. Carl (1931) left *P. cristata* pendent from the neotropical sections of the genus, in an "Anhang," suggesting a possible affinity to *P. cristatissima* and *P. scopulosa.* The combination of caducous leaves and ampliate leaves certainly suggests we are warranted in considering it to form a section separate from the others recognized by Carl. The wholly caducous leaves, and the strongly developed crista suggest a section only distantly allied to the Yokogurenses.

The discreteness of the Yokogurenses, as a section, became very clear during my study of *P. yokogurensis,* published in 1957. In 1956, when this manuscript was delivered to the editor, the Yokogurenses were recognized as a monotypic section, and diagnosed as above. In the meantime Inoue (1958, p. 86) had also recognized a section Yokogurenses, on much the same basis outlined above. Having fertile material at hand, he has been able to utilize additional characters, in part the number of antheridia per bract. Inoue also assigns to the Yokogurenses a second, distinctive, Japanese species, *P. furcifolia* Mitt.; this differs from *P. yokogurensis* chiefly in the distinctly bilobed leaves, with the attenuate lobes, rather than entire distal portion of the leaf, caducous.

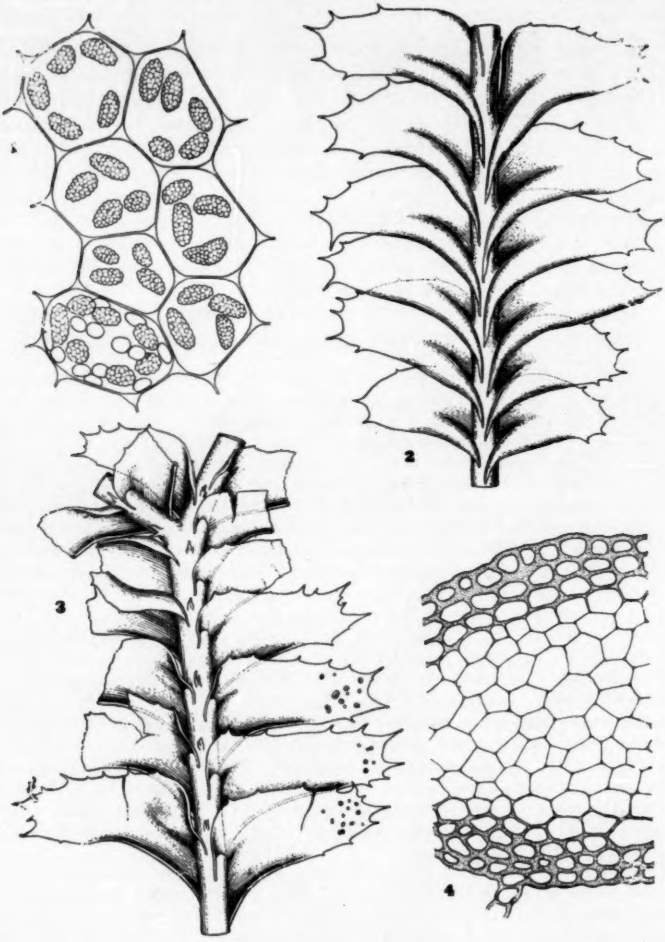

Fig. 37.—*P. yokogurensis fragilifolia*. 1. Median cells, with oil-bodies and (lower cell) chloroplasts (x 535); 2. Portion of shoot with persistent leaves in antical view (x 14.3); 3. Shoot-sector, with branch, postical aspect, showing dehiscence of distal halves of leaves, partly after initiation of propagula (x 14.3); 4. Part of stem cross-section (x 220). (All from material from Whitewater R. Gorge, South Carolina, *Schuster*.)

PLAGIOCHILA YOKOGURENSIS Steph.
Figs. 37-40

Plagiochila yokogurensis Steph., Bull. Herb. Boissier V, 104, 1897; Inoue, Bot. Mag. Tokyo 12:74, 1898; Stephani, Spec. Hep. II, 375, 1903; Horikawa, J. Sci. Hiroshima Univ. Ser. B., Div. 2, I:63, pl. VII; 12-17, 1931; Hattori, Bull. Tokyo Sci. Mus. No. 11:65, 1944; Schuster, J. Hattori Bot. Lab. 18:15, figs. 1-4, 1957; Inoue, J. Hattori Bot. Lab. 20:87, figs. 13, 14:1-10, 1958.

Plagiochila okamurana Steph., Spec. Hep. 6:190, 1921 (*fide* Hattori, 1952:23).

Plagiochila yokogurensis var. *kiushiana* Hattori, Bull. Tokyo Sci. Mus. No. 11:65, fig. 41, 1944 (*fide* Hattori, 1952:23).

Plagiochila curiosissima Horikawa, J. Jap. Bot. 11:411, fig. 1, 1935.

P. yokogurensis has been known only from Japan. The species is found from the broad-leaved "evergreen forest to the deciduous forest zone" and is reported as "not uncommon, preferably at low elevations," by Hattori (1952, p. 23). Judging from his reports (1944, 1952), *P. yokogurensis* is widely distributed and a variable taxon in Japan. The material studied confirms this impression. Indeed, the robust and dense-leaved plants of the species (as represented by Hep. Jap. Nos. 113, 16) are extremely different from the fragile, delicate, distant-leaved extreme (as represented by Hep. Jap. No. 181). These collections agree, however, in freely shedding the distal portions of the leaves, leaving more or less truncated stubs. The male plants issued as *P. yokogurensis* (Hep. Jap. No. 234) differ so widely from the foregoing collections (in leaf-form; absence of any tendency to shed the distal halves of the leaves) that I recently questioned (Schuster, 1957a) the propriety of considering them identical with *P. yokogurensis.* Hattori (in litt.) has since informed me that these plants do not represent *P. yokogurensis.* Inoue (1958), since this was written has referred the material to *P. makinoana.*

Allied to the Japanese plants is a widely distributed plant of the eastern slope of the Southern Appalachian mountains and the adjacent Piedmont and Coastal Plain. This plant has much the same facies as slender, fragile-leaved forms of *P. yokogurensis,* sharing with them a wide range of features: strongly nited texture when dry; a similar size; pseudodichotomous branching and an identical, basically ovate-falcate leaf-form, with the antical margin strongly arched, and the postical base short-decurrent; spinose marginal teeth, exhibiting a similar range in frequency; cell size and oil-bodies essentially alike. Hattori (1951, p. 78) describes the oil-bodies of *P. yokogurensis* and of the "var. *Okamurana* (St.) Hatt.", and illustrates them (Pl. V. figs. 9,21). Their range in number appears to be 5-13, or more frequently 6-12 per cell, with the size ranging from 3.5 x 4-8 μ or 3 x 4-8 μ to 2-3 x 2-6 μ in some cases. In the nearctic taxon there are somewhat fewer (4-7) oil-bodies per cell, and these are somewhat larger (4.5-5 x 6-9, rarely to 11 μ), suggesting a somewhat different genotype. The mode of asexual reproduction by means of fragmenting leaves, is well-marked in both the Japanese and nearctic

taxa. The similarities between the Japanese and nearctic populations are so marked that treatment of them as subspecies of a single old and polytypic species appears warranted, although Inoue (1958) suggests the American plant "may possibly be regarded as a distinct species. . ."

Since the preceding account was completed (and largely published, see Schuster, 1957a), I have had occasion to study topotypic plants, from Mt. Yokogura, Tosa, Japan (*T. Yoshinaga* 38, Aug. 1901). These plants are more robust than any others I have seen from Japan or from North America, ranging up to 4.3 mm wide; they tend to be somewhat olive-brown or brownish; the leaves are much more strongly falcate, with the distal portions spreading at an angle of up to 125-140°; the teeth of the leaf-margins are more sharply developed and coarser; the underleaves are bifid, with the acuminate lobes ciliate; the postical leaf-margins are very broadly reflexed, almost tubularly so; the freely fragile leaves are quite densely imbricate. On examining such luxuriously developed plants it seems impossible to consider them identical with our American plant. Nevertheless, these plants show a mere accentuation of features already suggested in the American plants. Under these conditions I am most reluctant to attempt a specific separation, especially since the weaker Japanese plants (such as fo. *curiosissima* (Horik.) Inoue; see Inoue, 1958) so closely approach our American phases. The status of such vicariads is notoriously difficult to evaluate, and one can only echo the opinion of Braun (1955) that in such Asiatic-American pairs of vicariads it is to "be expected, there are sometimes differences of opinion as to the status of the taxa."

If only mature and luxuriantly developed extremes of the Japanese and the American plant are studied (compare Fig. 40:1-2, 5-6 with 40:14-16) three obvious differences between them become apparent. Firstly, the Japanese plants have leaves that tend to be more strongly ampliate above the base, as compared with American plants; correlated with this, the distal portions of the leaves tend to be more strongly narrowed. Secondly, the larger Japanese plants often have relatively large underleaves (Fig. 40:1-2), whereas those of the American plant are always very small, rarely as large as in Figure 38:9-10. Only in weak plants of the Japanese entity are the underleaves minute. Thirdly, mature phases of the Japanese plant have large trigones (Fig. 40:3-4, 7-8), while the most robust phases of the American plant, from the most xeric habitats, still show small trigones, correlated with a tendency for the cells to become somewhat thick-walled (Figs. 40:17-20; 39:7; 38:2-3). Unfortunately, weakly developed (? juvenile) manifestations of the Japanese plant largely bridge these distinctions (Fig. 40:9-13).

KEY TO SUBSPECIES OF P. YOKOGURENSIS

1. Spinose marginal teeth of leaves sharper, the terminal cells (on mature leaves) 3-5 × as long as wide; mature leaves strongly ampliate, the length usually only 1.2-1.5 × width at the ampliate base; mature leaves with antical margin nearly straight or weakly concave, bearing up to 2-5 teeth on the distal 0.2-0.6 of the margin; robust plants with large and conspicuous underleaves; plants tending to have bulging, often subconfluent trigones. Japan. ....*P. yokogurensis* subsp. *yokogurensis* Steph.
1. Spinose marginal teeth of leaves less sharp, terminal cells (on mature leaves) 1.2-2.5, rarely 3 × as long as wide; mature leaves only moderately ampliate, the length normally 1.55-1.75 (rarely to 2.0) × the width at ampliate base; antical leaf-margin usually strongly concave, bearing only

1-2 teeth on distal one-third of margin; robust plants with minute underleaves, formed of 2-several cilia or laciniae; marginal cells ± equally thick-walled, the interior cells with small to scarcely bulging trigones. Eastern North America. .... *P. yokogurensis* subsp. *fragilifolia* Schuster.

Plagiochila yokogurensis subsp. *fragilifolia* Schuster.
Figs. 37-39; 40:14-20

Plagiochila yokogurensis subsp. *fragilifolia* Schuster, J. Hattori Bot. Lab. 18:18, figs. 1-3, fig. 4:14-20, 1957.

P. yokogurensi typicae similis; differt: foliis magis elongatis (1.55-1.75:1), plerumque minoribus et minus imbricatis, basi ventrali minime ampliata; foliorum dentibus minus acutis, cellulis terminalibus 1.2-2.5:1. Amphigastria minuta, e ciliis vel laciniis composita, haud lamellaria; cellularum trigones parvi, vix turgentes. Gemmae desunt. Typus: Whitewater R. Gorge, Oconee Co., South Carolina (*Schuster* 25162b).

Plants in diffuse patches, very *delicate, shining,* rather pellucid yellowish-green to green (becoming pale brownish with death of the older portions), with a distinct division into a creeping caudex and leafy aerial shoots. Leafy shoots *ca.* 2.8-3.6 (3.8) mm wide. Usually on bark of tree-bases, or on vertical rock-faces, and then (under optimal conditions) the elongate *3-5 times pseudodichotomous aerial shoots* forming pendent festoons, more rarely spreading from the substrate. Aerial shoot system diffusely, pseudodichotomously branched: the branch-system to 3.5-5.5 cm long, consisting of 3-5, occasionally 6-7 dichotomies. Main stems *ca.* 225-360 μ wide x (200) 240-260 μ high: cortex well-differentiated, 2-3 stratose, the outer layer of slightly tangentially flattened cells *ca.* 14-15 μ in diameter tangentially, thick-walled, the wall yellowish to brownish; medullary cells rather suddenly larger, thin-walled, hyaline, in *ca.* 10 cell-layers medially, *ca.* 22 to 22-25 x 25 to 28 x 35-45 μ in cross-section (averaging *ca.* 30 μ); stem medially *ca.* 14-16 cells high. Rhizoids absent or virtually so on aerial shoot-system. Leaves *weakly to moderately imbricate,* with an arched line of insertion, similar on main stem and branches, *narrowly ovate-falcate to triangular-falcate* (from *ca.* 1220-1370 μ long x 570-940 μ wide, subbasally to 1600-1900 μ long x 975-1150 μ wide; usually from *1.55-1.75, occasionally to 1.9-2.0 × as long as wide*); postical margin moderately *dilated above postical base,* but straight-margined from basal third of leaf to apex, the postical base short-decurrent (*ca.* 0.2-0.3 the length of the merophyte); antical margin with cnemis strongly developed, the *margin strongly concave; mature leaves thus ± strongly falcate,* the distal halves spreading at an angle of *ca.* 85-95 (110) degrees; leaf-apex normally characteristically narrowly truncate, coarsely 2-3 (4)-dentate; postical margin with additional (2) 3-8 smaller teeth, and distal one-fourth of antical margin often with 1-2 teeth (entire leaf thus with 6-13 teeth); teeth (when well-developed) moderately spiniform, 2-4 (5) cells long and 2 (-4) cells wide at base in most cases (except for the two larger, coarser distal lobe-like teeth), the *terminal cell* 1-2 (2.5) × *as long*

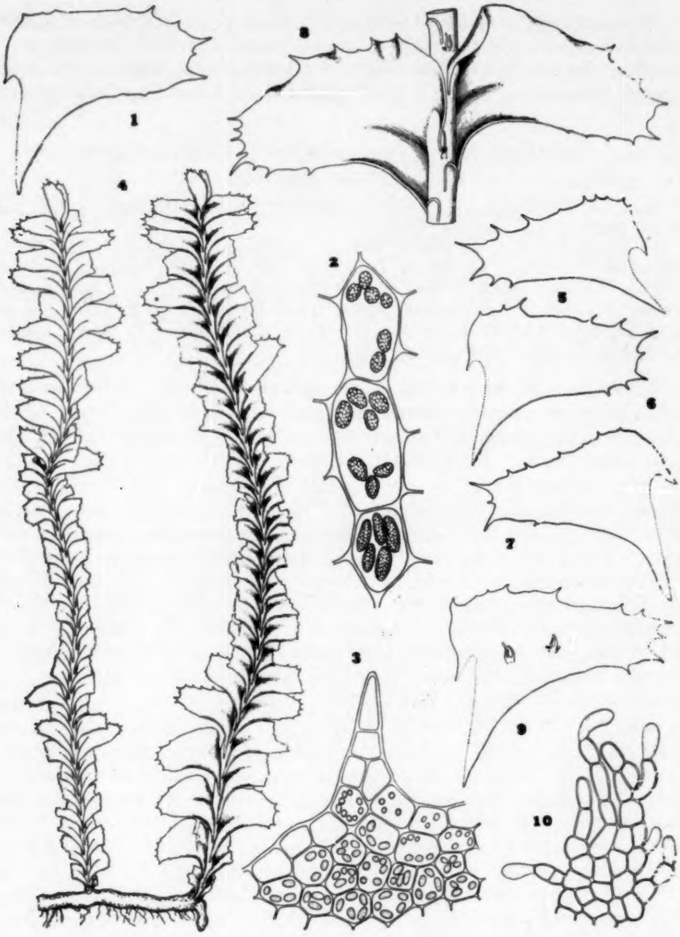

Fig. 38.—*P. yokogurensis fragilifolia.* 1. Leaf (x 20); 2. Cells near leaf base, along leaf midline (x 525); 3. Cells of leaf-margin, with tooth, showing absence of oil-bodies from some marginal cells (x 205); 4. Plant, showing characteristic growth of weaker extremes, with prostrate rhizome and unbranched, deciduous-leaved aerial shoots (x 5.3); 5-7. Leaves (x 18); 8. Part of robust shoot-sector, postical aspect, showing leaf insertion and small underleaf (x 18); 9. Large leaf and associated underleaves, drawn to same scale (x 15.2); 10. Underleaf of nearly maximal size (x 145). (1-3, 5-7, from plants from Whitewater R. Gorge, South Carolina, *Schuster;* 4. Washington, D.C., *Holzinger,* issued in Hep. Amer. No. 171 as *P. virginica;* 8-10, Eno R., near Durham, N. Carolina, *Schuster* 28200.)

as wide; line of insertion strongly elongate, the dorsal base conspicuously long-decurrent, the line of insertion *ca.* 800-975 (-1300) μ (*usually 1.0-1.2 × as long as subbasal leaf-width,* 0.55-0.7 the leaf-length). Juvenile leaves often much shorter, 1.1-1.4 × as long as wide, entire except for vestiges of the two coarse distal teeth (much as in *P. columbiana* leaves). *Asexual reproduction by leaf fragmentation,* the distal 1/2-2/3 of the leaf breaking off transversely as one or several large fragments; older portions of shoots usually malformed because of the persistence of only the truncate, irregular leaf-bases; in addition, lower leaf surfaces able to produce brood-plantlets from non-marginal leaf-cells. Cells with concave trigones, nearly isodiametric throughout the leaf, along postical margin 24-28 μ, *near leaf-apex 21-26 μ wide and long,* near leaf-middle equal in size or often smaller (17-24 *μ wide x* 18-25 *μ long*), near middle of base scarcely elongate, to 1.2-1.8 × as long as wide, 17-22 (24) μ wide x 21-32 μ long; cells of middle of postical margin nearly isodiametric, *ca.* (16) 20-25 μ, at base of postical margin little elongate (to 1.5-2.2 × as long as wide; 11-16 μ wide x 18-32 μ long); marginal 1, occasionally 2 rows of cells faintly equally thick-walled, the interior cells thin-walled and *with small to moderate, concave-sided trigones;* oil-bodies usually 4-7 per median cell, broadly to narrowly ellipsoidal and 4.5 x 6 to 4.5 x 8-9 μ, a few to 5 x 11 μ, a few spherical, *formed of many protruding oil-globules ca.* 1 μ in diameter, *thus papillose-segmented;* median basal cells with mostly 5-8 oil-bodies per cell of approximately the same size as in median cells; chloroplasts distinctly smaller than oil-bodies, *ca.* 4-4.5 μ; cuticle smooth. *Underleaves minute to small,* lanceolate and 5-6 (9) cells long x 2-4 cells wide at base, or consisting of 2-3 uniseriate cilia to 5-6 (9) cells long. *Plant habitually sterile.*

Type.—On damp shaded vertical walls of boulders in gorge of Whitewater River below lower falls, *ca.* 4-5 mi. NW. of Jocassee, Oconee Co., South Carolina (*Schuster* 25162b).

Distribution.—Widespread and often frequent; occurring from the eastern edge of the Appalachian Upland (there limited to the coves and ravines dissecting the edges of the Appalachian Plateau, occurring at an elevation of 2500 ft. or less), eastward throughout much of the Piedmont, and occasionally (along streams and in swamps) out to the outer Coastal Plain. The distribution of the subspecies is almost complementary to the essentially Appalachian *P. virginica* Complex, which rarely occurs below an elevation of 2400 ft.

The range of this taxon will probably be somewhat extended when all herbarium species assigned to *P. ludoviciana* and *P. virginica* are studied, since it has, in the past, been widely confused with these two species.

DISTRICT OF COLUMBIA: Washington (Underwood and Cook, Hep. Amer. No. 171, Aug. 1891; determined by A. W. Evans as *P. virginica* Evs., and published as such in Evans, 1896). VIRGINIA: Back Creek, at Highway No. 116, *ca.* 900 ft., Roanoke Co., moist calcareous bluff (*Patterson R*-395; as

P. virginica Evs.); Martinsville, Henry Co., along Smith R. at base of boulder in deciduous woods (*Patterson* 1450 (1954)); Big Spring, Lexington, Rockbridge Co. (*Carroll* 158 (1929); listed by Patterson, 1950, as *P. ludoviciana*); Dismal Swamp, near Feeder Canal at Lake Drummond, Norfolk Co. (*Patterson* (1954)); Portsmouth and Feeder Canals, by Lake Drummond, Dismal Swamp, Norfolk Co. (*Patterson* 1736, (1954)); bark of *Nyssa, Acer rubrum,* NE. side of Lake Drummond, Dismal Swamp, Norfolk Co. (*Schuster and Patterson* 34561, 34540, 34525, 34536); bark of *Acer saccharinum,* swampy woods 5 mi. NE. of Cypress Chapel, W. edge of Dismal Swamp, Nansemond Co. (*Schuster and Patterson* 34502, 34514). NORTH CAROLINA: Base of tree, Coolie Swamp near Bethel, Pitt Co. (*Anderson* 5934!); wet rock near waterfall, below Poor Man's Knob, near Hwy. 16, Wilkes Co. (*Blomquist and Anderson* 10041!); Raven Rock, NW. of Lillington, Harnett Co. (*Schuster* 28670); N. of Woodlawn, *ca.* 2.7 mi. N. of juncture of Routes 221 and 26, McDowell Co. (*Schuster* 29592a, 29584, 29585, 29574a, 29596); Laurel Hill, on Eno R., NW. of Durham, Durham Co. (*Schuster* 28216b, 28200, 28212a, 28216a, 28198, 34751, 28196, 37486); Laurel Hill on New Hope Creek, Duke Forest, SW. of Durham, Orange Co. (*Schuster* 28478); bark of *Nyssa aquatica,* swamp 1.5 mi. E. of Whiteville, Columbus Co. (*Schuster and Blomquist* 29233, 29225, 29484a, 29483a, 29234a, 29228; *Schuster* 29491; *Schuster, Blomquist, Bryan* 29980c, 30045); shell marl on Island Creek, near Trent R., Jones Co. (*Radford* 5918); Eno R., near crossing of Huckleberry Springs Rd., N. of Durham, Durham Co. (*Blomquist* 11492); Christians Mill, Eno R., N. of Durham (*Blomquist* 18838); Hickory Nut Falls, Chimney Rock, Rutherford Co. (*Blomquist, Correll, Garren* 7786a); Laurel Hill, Orange Co. (*Blomquist* 7322); Lime Rock, 2.4 mi. W. of Richmond Hill, Yadkin Co. (*Anderson* 6544); Palisades, Moores Springs, Stokes Co (*Schallert,* 2853); along Eno R., W. of Hwy. 501, *ca.* 5 mi. N. of Durham, Durham Co. (*Schuster and Blomquist* 28412); Raven Rock, along Cape Fear River, N. of Mamers (*Anderson* 9642!); Slopes of Melrose Mt., Saluda (*Evans,* 1929! in herb. Y as *P. ludoviciana*). SOUTH CAROLINA: Below Lower Falls of Whitewater R., *ca.* 4-5 mi. NW. of Jocassee, Oconee Co. (*Schuster* 25110, 25162, 25169c, 25169, 25164, 25110, 25162b, type; *Schuster* 40911, 40918; *Anderson* 8917); Reedy Cove Falls, near Nimmons, Pickens Co. (*Anderson* 8817); gorge of Whitewater River, S. of Lower Falls, *ca.* 3 mi. N. of Jocassee, Oconee Co. (*Schuster* 27827, 27828, 27830a); base of tree, wooded swamp 8 mi. S. of Bamberg, Bamberg Co. (*Schuster* 33980, 33983).

The published reports of *P. ludoviciana* from North Carolina (Blomquist, 1936), from Stokes, Orange, Durham Cos. are based on the material here listed under *P. y. fragilifolia.*

Ecology.—P. yokogurensis subsp. *fragilifolia* occurs under two widely different sets of conditions: (1) primarily over shaded, damp rock-walls, usually in gorges or along streams; (2) at the bases of tree trunks along rivers. Although most often on noncalcareous rocks, one collection is cited from a "moist calcareous rock by stream." The plants occur largely, but not exclusively, in areas with deep shade, particularly on shaded moist ledges, and on the shaded vertical faces of boulders, along rocky, cascading streams, sometimes in the shade of *Kalmia, Leucothöe editorum, Rhododendron maximum* and *Tsuga canadensis,* or under deciduous trees. The plants appear to be able to undergo ecesis only in areas with a relatively low saturation deficit,

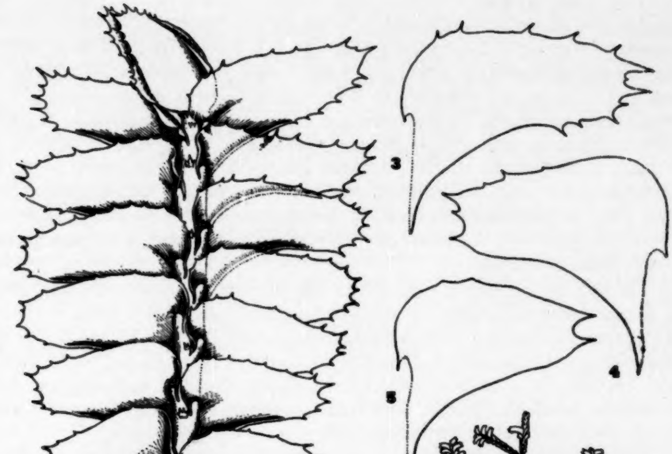

Fig. 39.—*P. yokogurensis fragilifolia.* 1. Shoot, postical aspect (x 16.5); 2. Shoot-sector, antical aspect (x 16.5); 3-5. Leaves (x 19); 6. Plant approaching maximal development, showing pseudodichotomous forking and fragmentation of all but juvenile leaves (x 1.5); 7. Apex of postical leaf-margin (x 160). (1-5 from the poorly developed plants issued as *P. virginica* in Hep. Amer. No. 171, from Washington, D.C.; 6. Whitewater R. Gorge, S. Carolina, *Schuster* 25010; 7. Eno R., N. Carolina, *Schuster* 28200.)

and therefore have much the same ecological "requirements" as *P. caduciloba* and *sharpii* (with which the species may occur in the Appalachian gorges). Other associated species in the Appalachian gorges are *Radula tenax* and *sullivantii, Metzgeria hamata, Harpalejeunea ovata* and *Lejeunea lamacerina gemminata,* and occasionally the fern *Trichomanis petersii.* Less frequently associated, on ledges and rock walls, are *Metzgeria conjugata, Lejeunea laetevirens, Leucolejeunea clypeata, Lophocolea cuspidata, Radula andicola, Rectolejeunea maxonii* and *Plagiochila asplenioides.* The species also occasionally is found on shaded, humid boulders along streams (*e.g.,* the lower gorge of the Whitewater R., S. C., *Schuster* 40918), associated with *Plagiochila sharpii, Radula obconica, Metzgeria conjugata, Lejeunea laetevirens, Cololejeunea biddlecomiae,* and the locally rare *Lophocolea muricata.*

On the rocky banks and ledges along the Piedmont streams, some of the preceding species are often associated (*Leucolejeunea clypeata, Metzgeria conjugata* and *furcata,* occasionally *P. asplenioides*), but more frequently one finds *Plagiochila undata, Radula obconica, Metzgeria myriapoda;* in very damp situations *Porella pinnata,* in drier situations *Frullania plana,* and, rarely, when the ledges become soil-covered as succession proceeds, *Reboulia hemisphaerica.*

The second, less frequent mode of occurrence is on soil at the bases of trees and on bark on the lower trunks of trees, either in swamps (as near Whiteville, N. C.; and as in the Dismal Swamp), or along rivers (Trent R., N. C., there both at the bases of trees, and on clayey soil, as well as, exceptionally, on shell marl). When at the bases of trees in the warm outer Coastal Plain, the species may occur with *Porella pinnata.* On bark proper, it is found with a wide variety of hepatics, some widespread in occurrence (*Frullania asagrayana, Radula obconica, Bazzania trilobata, Jamesoniella autumnalis, Leucolejeunea clypeata*), others of distinctly southern or tropical affinity (*Plagiochila dubia, Radula caloosiensis, Rectolejeunea maxonii, Lejeunea flava, Euosmolejeunea rigidula,* and exceptionally, at Whiteville, N.C., also *Lopholejeunea muelleriana*). The plant is particularly frequent on bark in a large swamp E. of Whiteville, N.C., where it is found on *Nyssa aquatica,* with all of the preceding species, as well as with the subtropical epiphytic orchid, *Epidendrum conopseum,* at its northernmost known station.

Differentiation.—This distinctive taxon differs from all our species in the fragile leaves and in the associated strongly falcate leaf-form. It is the only regional species in which the distal portions of the leaves (or at least of the majority of them) are deciduous, usually across a line near the middle, leaving a series of subequally long, truncate remnants on the older portions of the stem. The delicacy of the leaves is readily evident when the plants are handled. In addition to asexual reproduction in this manner, the leaves also produce brood-plantlets from the postical leaf-surfaces (indicating an affinity of the plant to the Sectio Contiguae). The reproductive pattern of this

species therefore represents a specialization over the type of the *P. virginica* Complex, in which the leaf-surface produces small plants, which on attaining a certain size, break free and are disseminated. In *P. yokogurensis* subsp. *fragilifolia* we find that the distal one-third or more (to which production of brood-plantlets is usually limited) breaks free before the initiation of the propagula or when the brood-plantlets are exceedingly small (usually 1-8-celled globular protuberances); hence the two chief types of asexual reproduction (caducous leaf type, brood-plantlet type) are combined in this species.

The degree of development of caducous leaf-apices undergoes considerable variation. I have seen thousands of individual plants in the field; in each case, some leaves (or portions thereof) were clearly caducous. This readily evident character of the species allows its recognition with the naked eye. Under some conditions, the development of the caducous leaves becomes almost universal, e.g. in the material from Harnett Co., North Carolina (*Schuster* 28670) the writer found that most shoots had lost between 70-90 per cent of the distal portions of the leaves; in some cases young leaves, up to the shoot tip, were caducous—except for a ragged irregular basal portion—resulting in flagelliform, unrecognizable shoots.

The numerous nearctic collections lack sex organs. However, typical *P. yokogurensis,* from Japan, produces juvenile perianths, described by Hattori (1944) as urceolate, with complanate and densely spinose mouth. Judging from his fig. 41h, the mouth is strongly obliquely terminated, with the antical keel of the perianth much longer than the postical (as in some species of the Sectio Hypnoides).

The total sterility of the nearctic taxon is interesting, but not without parallel. *Herberta sakuraii* produces both perianths and androecia in the oceanic portions of Europe, and in Alaska; the plants from the Southern Appalachians ("*H. tenuis* Evans," but not specifically separable from either *H. hutchinsiae* or *H. sakuraii*) are almost constantly sterile. This tendency for the eastern American representatives of ancient, early Tertiary, or pre-Tertiary species to be totally sterile deserves further study.

P. yokogurensis subsp. *fragilifolia* is not closely allied to other North American species, although it has been confused with *P. virginica* (of the Sectio Contiguae) and *P. ludoviciana* (of the Sectio Crispatae). Superficial similarities also exist to *P. hypnoides* of the Sectio Hypnoides.

When the plant is typically developed, the freely fragile leaves at once distinguish it. In the case of old herbarium specimens which may be much battered, it is often admittedly difficult to decide whether a plant has normally fragmenting leaves, or whether the dry plants have merely been crushed. As a consequence, the manner of reproduction of *P. yokogurensis* is a less effective systematic character for the worker who restricts his activity to herbarium specimens, than for the worker who is familiar with the group in the field. Some of the considerable confusion to which this isolated species has been subjected can be attributed to a misunderstanding of the unique reproductive mode; "artificial" fragmentation commonly results from handling of dry specimens. In addition to the anomalous repro-

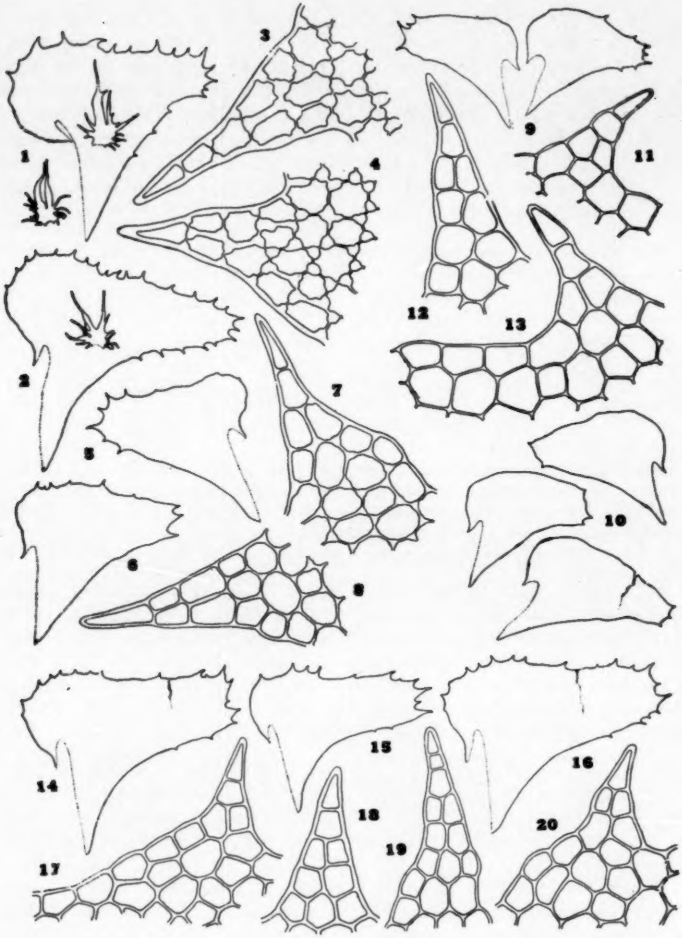

Fig. 40.—1-13. *P. yokogurensis* subsp. *yokogurensis*. 1-2. Leaves and underleaves; 3-4. Teeth from leaves; 5-6. Leaves; 7-8. Teeth of leaves; 9, 10. Leaves; 11-13. Teeth of leaves; 14-20. *P. yokogurensis* subsp. *fragilifolia*. 14-16. Leaves; 17-20. Teeth of leaves. (Leaves and underleaves all one scale, (x 13); cells all one scale, (x 218); 1-4 from Hattori's Hep. Jap. Exsic. No. 16, a dense and large-leaved phase; 5-8, from Hattori's Hep. Jap. Exsic. No. 113, a dense and persistent-leaved phase; 9-13, from Hattori's Hep. Jap. Exsic. No. 181, a small, remote-leaved phase with fragile leaves; 14-20, from Eno R., N. Carolina, from the maximal-sized American extreme, *Schuster* 28220.)

ductive mechanism, there are a series of differences that separate the species from the at times superficially similar *P. virginica,* with which confusion is most likely. Among these are: (a) the shiny texture, when dry, of *P. yokogurensis; P. virginica* is quite dull when dry; (b) larger leaf-cells, particularly in the apical region of the leaf; (c) the more distinctly falcate, and considerably narrower leaves of mature plants of *P. yokogurensis* subsp. *fragilifolia;* (d) the concavely arched antical margin of mature leaves, with the antical bases very long-decurrent on robust plants.

P. yokogurensis agrees with *P. virginica* in one important respect, however. It has the leaves postically short-decurrent, with the decurrent strip not forming a crista or water-sac. In this respect, *P. yokogurensis* differs at once from both *P. hypnoides* and *P. ludoviciana.* The shiny texture when dry; the tendency towards development of falcate leaves; the usually slight development of trigones are other characters in which *P. yokogurensis* differs from these two species. When well-developed, however, the freely pseudodichotomous forking of the aerial shoots strongly suggests well-developed plants of *P. hypnoides* and *P. ludoviciana.* This similarity is further emphasized by the long and conspicuously decurrent antical leaf bases, and by a tendency for the leaves to be somewhat more closely shingled than in the Contiguae. This tendency is less well-marked in the nearctic subspecies of *P. yokogurensis* than in the typical, Japanese subspecies, but can occasionally be noted. For instance, in the maximally developed plants from Eno R., North Carolina (*Schuster* 28200) some shoots show a virtual overlap of the ampliate leaf-bases, thus hiding the stem beneath. Even such extremes fail to show the crista-formation distinguishing the Sectio Hypnoides.

Occasionally, under difficult conditions, *P. y. fragilifolia* has virtually unramified aerial shoots, and may have scarcely falcate leaves. Such plants are quite subject to confusion with *P. virginica.* The material of *Anderson* 9642 (North Carolina) is pertinent in this connection. The plants have the facies of *P. virginica,* and its small size—but are rather strongly shiny, have (on the most robust shoots) somewhat narrower and more falcate leaves, and show (on most shoots) some leaves that break along a line near their middle. However, the plants are decumbent in growth, only 2.5-2.8 mm wide, and nearly simple, with only occasional, monopodial branches.

Our subspecies appears to be most nearly related to the "var. *kiushiana*" Hattori (Hattori, Bull. Tokyo Sci. Museum No. 11: 65, fig. 41, 1944 = fo. *kiushiana* (Hatt.) Inoue (see Inoue, 1958) which shows the following characters: fragile cauline leaves, contiguous to moderately imbricate, of virtually identical form as in our subspecies, the free apices spreading at an angle of 75-90°, somewhat secund, leaves oblong-trigonous in shape, 1.5-1.8 mm long x 1.3-1.5 mm wide at base; antical margin edentate to 1-2-dentate below apex; postical margin dilated at base and with *ca.* 3 strict teeth, the distal half of postical margin with 1-3 teeth; spinose teeth narrowly acute to acuminate; apex subtruncate, with 2-3 teeth (the third tooth, when present, smaller); cells everywhere subequal, 25-35 μ long x 20-25 μ wide, becoming longer near base and 25 x 35-45 μ long. Most of these characteristics appear in our taxon, to a greater or lesser extent. However, certain features appear to set off our plant: the often more

widely spreading leaves; the smaller leaf-size; the slightly smaller median cells, which are less elongate basally; the less extreme development of the trigones; the less spinose teeth of the leaves, with the terminal cells usually less than twice as long as wide. In *P. yokogurensis* var. *kiushiana* Hatt. the postical bases are often strongly reflexed, but not so fully as in the typical species (and never appear to be reflexed and rolled outward to form a tubular fold). Furthermore, the leaves are distinctly less broadly dilated, and closely approach those of *P. yokogurensis* subsp. *fragilifolia* in shape. In these two features, the var. *kiushiana* rather closely approaches our native subspecies.

Sectio VII. PARALLELAE Carl

Plants green, relatively robust (to 4-5 mm wide). Branching *loosely tree-like, copious,* initially partly axillary and intercalary, but on mature shoot sectors *wholly or virtually wholly terminal;* initial branches of the shoot system ± monopodial, but the distal branches normally *furcate, pseudodichotomous, numerous; innovations below perianth usually lacking* if gynoecia situated on small ultimate branches; stems with cortex 3, occasionally locally 4-stratose. *Leaves remote to contiguous, when moist flatly spreading, when dry tubularly convolute, very narrow* (2.0-2.5, rarely 3.0 × as long as wide), narrowly rectangular to *lingulate, the antical and postical margins nearly parallel, the leaf-apex usually subtruncate, the postical margin sharply but very narrowly reflexed, short-decurrent;* leaves sparsely spinose-dentate, the antical margin entire, the *teeth largely limited to the apex and distal one-fourth of the postical margin.* Cells within apex subisodiametric, basally becoming relatively elongate, the marginal ± strongly elongate, averaging at least 1.5-2 × as long as wide, commonly set off as a discrete border from the nearly isodiametric interior cells (by the strong thickening of the tangential walls between the marginal and interior cells); median cells becoming elongate and basal cells averaging to twice as long as wide (but *not forming a vitta*); trigones distinct, *often large,* not or hardly confluent; occasional intermediate thickenings present. Oil-bodies sublinear, usually *formed of a few coarse segments* in one (sometimes medially in two) rows. *Underleaves virtually absent,* of a filiform cilium, rarely very small. *Asexual reproduction by means of leafy propagula* of the postical leaf-surface.

Perianth (immature only known) obdeltoid to triangular in lateral profile, widest at the bilabiate, ciliate mouth, laterally compressed above and along the postical keel, the dorsal keel usually narrowly winged with an entire wing, occurring at apices of main or more often on short lateral shoots.

This section includes the single regional species, *P. diffusa.* The development of a marginal border of prominently elongate cells, the few-segmented nearly linear oil-bodies, the dendroid, deliquescent branching, and the leaf-form (with the leaf *not* widest above the

immediate base, but subparallel throughout, hence never ovate), set the group off from the *P. virginica* complex (Sectio Contiguae). *P. diffusa* appears most closely similar, among our species, to *P. floridana*, in the Contiguae, but the relationship is superficial. As Carl (1931) has emphasized, branching is such that an individual leading stem is dissolved above into repeatedly furcate (pseudodichotomous) lateral branches. This is illustrated in Fig. 42:6, although this hardly typifies the most copious extent of ramification to be found. The leaves are always remote to barely contiguous when moist. They are so inserted ventrally that the short, narrow, decurrent strip, and the postical margin immediately above are characteristically, but narrowly, sharply reflexed (usually even more sharply so than in Fig. 41:7), the short lines of insertion of the leaves being strongly acroscopically arched. As a consequence, in drying, the leaves become nearly or quite tubularly convolute, acquiring in extreme cases a linear aspect. In our species the leaves are not strongly falcate; this is also characteristic of the other species of the section, except for *P. falcata* Steph., in which they are moderately falcate. Androecia are unknown in regional material of our species; they are intercalary in the neotropical species assigned to it by Carl.

Male plants (*P. diffusa* of Cuba) are equally strongly, deliquescently branched as are the female plants, showing repeated bifurcation. The very compact androecia are situated usually at or near the bases of branches of the third or fourth order, and appear to proliferate distally. The androecia, because of their basal or subbasal position on the forks of a repeatedly branching system are almost always gemminate; only rarely are solitary androecia produced. In some cases they are basal on each fork of a pair of branches; in other cases 1-3 pairs of more or less normal leaves are produced on each fork before the androecia are initiated. The 6-8 pairs of bracts become smaller and more rudimentary distally, hence the antheridial spike narrows distally, much as is typical in most other Plagiochilae; the bracts are imbricate and very strongly ventricose, much smaller than normal leaves, with only the distal portions of the bracts obliquely spreading to reflexed, and bearing a few small teeth. The vegetative proliferations at the androecial apices very commonly undergo one or two bifurcations, only rarely appearing to remain abbreviated. The plants from Ecuador, assigned by Herzog (1952) to *P. diffusa* have gemminate androecia that do not proliferate distally (see Herzog, *loc. cit.*, fig. 13a). It is questionable whether these plants should be assigned to *P. diffusa*. Carl states that the species assigned to this complex possess intercalary androecia, and the androecial plants from Cuba, assigned to *P. diffusa* by Evans (in herb. Yale) also possess uniformly intercalary androecia.

I have delimited the Parallelae more narrowly than Carl (*loc. cit.*, p. 78) has done, and limit it to species with remote to contiguous leaves. On that basis such species as *P. confertifolia* Tayl. (see Carl, *loc. cit.*, fig. 9i) should probably be removed from the Parallelae.

PLAGIOCHILA DIFFUSA Stephani

Figs. 41, 42

Plagiochila diffusa Stephani, Bull. Herb. Boissier II (2):870, 1902.

Plagiochila smallii Evans, Bull. Torrey. Bot. Club 32:180, pl. 5, figs. 1-8, 1905 (new synonym).

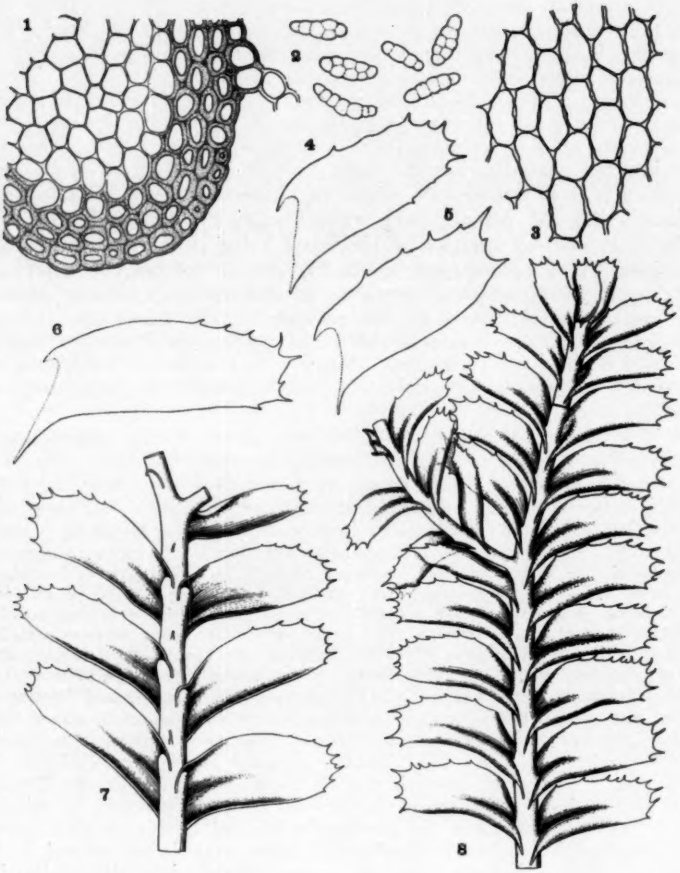

Fig. 41.—*Plagiochila diffusa* Steph. 1. Part of stem cross-section (x 230); 2. Oil-bodies (x 1000); 3. Median cells of mod. *pachyderma* (x 208); 4-5. Leaves, in fig. 5 from a branch (x 12.5); 6. Stem leaf (x 14); 7. Robust shoot-sector, postical aspect, with *Frullania*-type branch above and narrow subtending leaf (x *ca.* 10); 8. Large shoot-sector, antical aspect, with a *Frullania*-type branch at the left; several leaf-pairs omitted above (x *ca.* 8). (Figs. 1, 6-8, from type of *P. smallii* Evs.; 2, Timms Hammock, Florida, *Schuster* 22850; 3-5, from cotype of *P. diffusa* Steph. in NYBG.)

Plants in extensive, usually loose, prostrate patches, *pure to deep green,* with the stems often brownish. Aerial, leafy shoots at maturity 3.2-4.8, rarely 5 mm wide, the *slender flexuous stems rigid, ca.* 320-350 μ thick, 3-6 cm long, initially diffusely, sparsely monopodially branched, ultimately *freely furcately branched;* branches obviously smaller and less in diameter than the main axis, often spreading obliquely at approximately a 45-50° angle from main stem; often without innovations from below the terminal perianth. Cortex 3, locally 4-stratose, thick-walled, the cell-walls brownish, the cells elongate; interior cells thin-walled, quite elongate; stem as a whole 14-16 cells high. Rhizoids absent on aerial shoots. Leaves inserted by a rather strongly, acroscopically curved line of insertion, *distant to approximate,* but never imbricate, *short-decurrent by a narrow strip postically, the strip narrowly but sharply reflexed,* moderately long-decurrent antically; leaf-shape essentially *obliquely rectangular to lingulate, virtually parallel-sided,* spreading horizontally on each side at an angle of (45) 50-75° with stem apex, varying from 700 μ wide x 1650 μ long (2.35 × as long as wide) to 750 μ wide x 1750 μ long (2.45 × as long as wide) in type of *diffusa,* to a maximum of 900 μ wide x 1800-2100 μ long (2.0-2.33 × as long as wide), and occasionally to *1000-1200 μ wide x 2500-2700 μ long (2.25-2.5 × as long as wide).* Leaves with *apex usually rounded-subtruncate,* and with 3-4 teeth, the teeth often entirely unequal, but the larger scarcely large enough to suggest bilobing; postical margin nearly straight to slightly arched, not dilated just above base, usually with 1-4 small spinose teeth on distal one-half to two-thirds of margin; antical margin nearly straight, reflexed to slightly revolute for most of its length, the cnemis distinct; marginal teeth mostly 2-5 cells long and 2-3, occasionally 4 cells wide at base, the larger apical ones sometimes 6-10 cells long x 3-7 cells wide; apices of teeth usually with 2, occasionally 3 cells in a row, the cells mostly 1-1.8 × as long as wide. Branch leaves similar in shape to leaves of main stem, smaller, usually with 5-8 teeth. Cells of the leaf-middle from 18-20 x 32-35 μ to 20-22 x 36-38 μ (type of *diffusa*) to 23 x 37 μ (type of *smallii*); of the margins below the immediate apex 14-17 x 42 μ (type of *diffusa*) to 15-16 x 28-35-40 μ (type of *smallii*), of the apex within the border of elongate cells *ca.* 17-21 μ wide x 20-26 μ long; of the leaf-base *ca.* 23-27 μ wide x 42-50 μ long (averaging somewhat less than twice as long as wide; not forming a discrete vitta); cell-walls thin and trigones medium-sized and to somewhat bulging, with occasional intermediate thickenings of the longer longitudinal walls; *marginal cells in* 1, *occasionally* 2 *rows with the walls parallel to the margins very strongly thickened,* setting off the marginal cells as a discrete, sharply defined border of very evidently elongate cells; cuticle smooth; oil-bodies relatively small, mostly 6-10 per median cell, narrowly ellipsoidal to linear, formed of single (rarely medially 2) rows of coarse segments; the oil-bodies thus usually transversely segmented into 2-4, occasionally 5-7 segments; oil-bodies mostly 3 x 5 to 3 x 8 μ, a few to 3 x 9 or 2.5

x 11 μ; chloroplasts *ca.* 4.5 μ, their area averaging *ca.* the same as that of the oil-bodies. *Underleaves rudimentary,* of 1-2 ciliary segments, inconspicuous. Asexual reproduction present, *by leafy propagula* of the postical leaf-surface.

Frequently with female inflorescences, but male inflorescences unknown in our plants. Perianths terminal on elongate main or *more often on the ultimate lateral branches.* Female bracts like stem leaves, often slightly wider basally, the postical margin usually more fully and more strongly dentate, *ca.* 920-1200 μ wide x 1800-2500 μ long, little or not larger than vegetative leaves. Perianth (juvenile) campanulate, *ca.* 1-1.4 mm wide near mouth x 1.2-2.0 mm long, not strongly, laterally compressed above, the *dorsal keel narrowly winged,* at least below, the wing entire; postical keel shorter than antical, the mouth oblique; mouth broad (the perianth widened to the mouth), bilabiate, each lip with *ca.* 16-20 close to approximate, sharply aciculate teeth, the teeth usually 6-12 cells long (uniseriate terminal filament usually 3-7 cells long), 2, rarely 3-4 cells wide at base, formed of thick-walled cells *ca.* 15-20 μ wide x 20-25 μ long; the slender terminal cells *ca.* 15-18 x 25-32 (36) μ.

Type.—Cuba (Wright, Hepaticae Cubensis Wrightianae) (type of *P. diffusa*); cotype material studied in NYBG and Yale University. Type of *P. smallii* in NYBG (between Cutler and Camp Longview, S. of Miami, in hammocks near the Homestead trail, Dade Co., Florida, *Small and Carter* 1411!).

Distribution.—Widespread but not abundant in Dade and Monroe Counties, Florida (*i.e.,* the strictly tropical portions of Florida in the frost-free regions), and apparently more widespread in Cuba (type of *P. diffusa*), the Bahamas, the Antilles, Bermuda, and Puerto Rico (Pagan, 1939).

In Florida confined wholly to the so-called "Everglade Keys" and occurring at one time in the limestone region around Biscayne Bay, and on the higher of the Florida Keys. The species is now extremely rare and local, except in two hammocks (Timms Hammock and Ross-Costello Hammock), being evidently extinct on Big Pine Key and elsewhere on the Florida Keys, and in the Brickell Hammock region (in all of which I have repeatedly searched for the plant) from where it has been eliminated by uninhibited destruction and fires accompanying real-estate developments. In the two remaining hammocks where it is common, clearing accelerates further extinction. Apparently absent in the hammocks of the Long Key Pineland, within the Everglades National Park.

FLORIDA: Brickell Hammock, S. of Miami (*E. G. Britton* 87); Miami (*Rachel Love,* 1916); Costello Hammock near Silver Palm, Dade Co. (*Small and Carter* 2817a); Ross-Costello Hammock (*Small and Mosier* 5267; *Schuster* 38102, 38104); Timms Hammock, N. of Bauer Drive, near Homestead (*Schuster* 22850; *Small and Mosier* 5289, 6189); between Coconut Grove and Cutler (*Small and Carter,* 1388); in Everglades near Camp Longview (*Small and*

Wilson, 1520); Hattie Bauer Hammock (*Small and Mosier* 5307); Brogdon Hammock (*Small and Mosier* 6234); Nixon-Lewis Hammock (*Small and Mosier* 5242, 6239); Horton Hammock (*Small* 7013); Cox Hammock (*Small and Mosier* 5261, 5266); Goodburn Hammock (*Small and Mosier* 5240, 5173a); Sykes Hammock (*Small, Mosier and Small* 5253); Big Pine Key, Monroe Co. (*Small, Carter and Small* 3685b); Redlands Hammock, NW. of Homestead, Dade Co. (*Schuster* 42101a, 42130c, 42131; with *Lejeunea minutiloba, Ceratolejeunea cubensis, Radula australis, Rectolejeunea brittoniae, Trichomanis punctatum*).

Outside of our area known from: CUBA: Banao Hills, Sta. Clara (*Bro. Clement* 20!); La Prenda, Guantanamo (*Br. Hioram, Ch. Maurel* 5067; "probably," *fide* Evans); La Prenda, Oriente (*Bro. Hioram, Ch. Maurel* 2606; *Bro. Hioram* 4118); Las Ninfas (*Bro. Hioram* 2022; "*near Plagiochila diffusa* Stephani," *fide* Evans); slope of Puton del Mate, *ca.* 1200 m. Junas (*Fre. Leon*, 12297). BERMUDA: Paynter's Hill (*Howe, July 5, 1900*); cave, Paynter's Vale (*E. G. Britton* 360). BAHAMAS: New Providence, shores of Lake Cunningham (*Brace* X2).

Clebsch (1954) has also reported this species from the Smoky Mts. in Sevier Co., Tennessee, basing his reports on a determination by T. C. Frye. The pertinent specimen represents the unallied *P. echinata.* Since *P. diffusa* is the most nearly exclusively tropical species of the genus in North America, and the only one not extending north of the Everglade Keys and Biscayne Bay region, its occurrence in the Smoky Mts. would be a fantastic range extension.

Occurrence.—A species with a high requirement for shade and moisture, limited, at least in our region, to the denser, more humid hammock forests, where it apparently does not undergo ecesis above the basal butts of trees. Usually on thin soil, often over coral limestone and on damp humus, often at the bases and around the exposed roots of broad-leaved evergreen trees. Most commonly in and around humid lime sinks and limestone grottos, associated with *Tectaria heracleifolia* and *minima.*

Variation.—*P. diffusa,* judging from the limited available material is a species exhibiting little variation. The plants show certain typical features not usually found in our other species; they always appear to have long internodes (mod. *laxifolia*). Our only other species with habitually distant leaves is *P. tridenticulata,* which is quite unrelated.

Although the plants always appear to occur in the hammock forests, leptodermous extremes are unknown. Even in the mod. *mesoderma* (Timms Hammock, *Schuster* 22850), the border of marginal cells, set off by thick tangential walls between the marginal and inner rows, is extremely well developed. This border extends into the teeth of the leaves, where the cells may become more evenly thick-walled. At the base of the teeth the longitudinal walls of the cells below the teeth proper may also be thick-walled, often irregularly so, owing to the development of more or less discrete intermediate thickenings.

The plants, in my experience, always occur as a mod. *viridis-laxifolia-denticulata*—with the postical margins of the leaves virtually never overlapping the antical margins of the leaves lying immediately anterior to them.

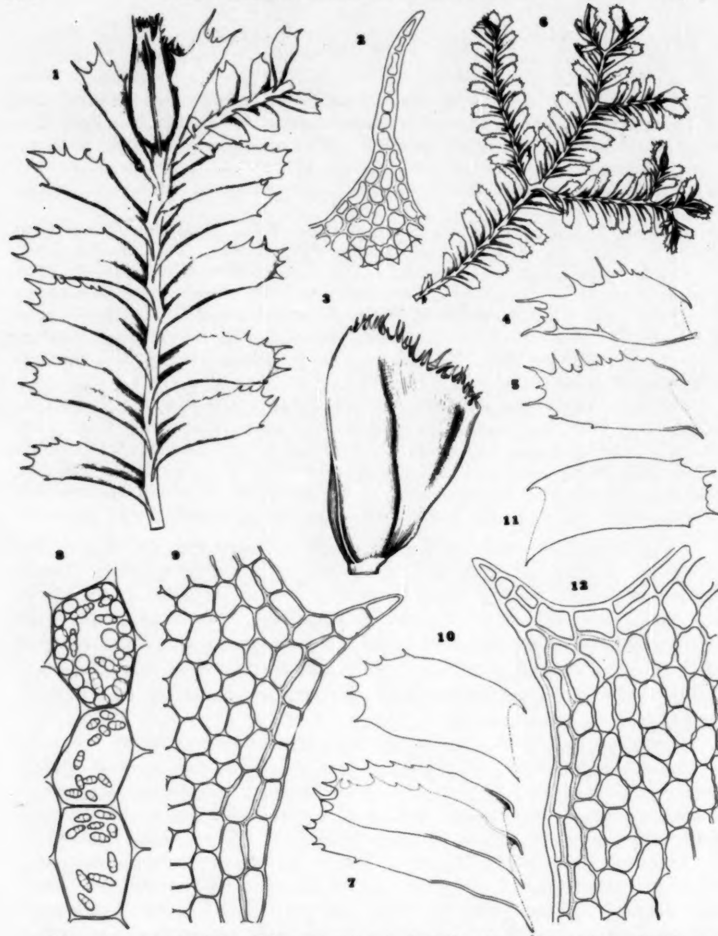

Fig. 42.—*Plagiochila diffusa* Steph. 1. Leading branch, with perianth and two subfloral innovations, one of them embryonic; phase with strongly spinose leaves (x 9.5); 2. Large tooth of perianth-mouth (x 140); 3. Lateral aspect of perianth, the dorsal carina at left (x 18); 4-5. Female bracts (x 11); 6. A medium-sized aerial shoot-system, each ultimate branch ending in a gynoecium (x 2.5); 7. Two leaves of main stem, postical aspect (x 11); 8. Median cells with oil-bodies and, above, chloroplasts (x 520); 9. Cells along postical margin, below apex (x 175); 10. Branch leaf (x 11); 11. Stem leaf (x 11); 12. Cells along postical leaf-margin, below apex (x 170). (Figs. 1-7, Costello Hammock, Florida, *Schuster* 38102; 8-9, Timms Hammock, Florida, *Schuster* 22850; 10, from type of *P. smallii;* 11, from plants from Banao Hills, Cuba; 12, from type of *P. diffusa,* in the Hep. Cub. Wright.)

Differentiation.—*P. diffusa* stands rather isolated among our species of *Plagiochila.* It is one of our largest species (width 4-5 mm), yet it is a relatively delicate species, because of the distant, narrow, elongate leaves, and the considerable shrinkage in drying. Mature plants are very different from all our other species in the freely pseudodichotomous, deliquescent, dendroid branching.

The narrow, nearly parallel-sided leaves eliminate all but *P. austini* and *floridana* from confusion. From these *P. diffusa* differs not only in the freely furcate branching, but also in (1) the coarsely segmented, sublinear oil-bodies; (2) the development of a sharp marginal border, owing to the fact that the inner tangential (but not radial) walls of the marginal cells are strongly thick-walled and the cells elongated (averaging about twice as long as wide), contrasted to the nearly isodiametric cells found within the leaf-margins. This border of elongate cells serves to separate the species not only from *P. austini* and *floridana,* but from our other species as well. In addition to these cytological differences, *P. diffusa* also differs from these two species in the constantly distant, at best somewhat approximated leaves—giving the plants a characteristic appearance. The similarities between *P. diffusa* and *P. austini* and *floridana* are obviously of a general nature. The plant differs from both *P. floridana* and *austini* in its superior size. It differs considerably in facies from *P. floridana* because the leaves are widely spreading (at an angle of 50-65° or even 70° rarely only 45° and then only near the shoot-apex), and also appears to differ from that species in the vestigial underleaves. Although the angle at which the leaves spread, and the narrow leaf-form suggest *P. austini,* several characters serve to separate it from the latter, among them: the brighter green color and dull texture; free terminal branching; the lack of any tendency to produce bilobed leaves, even on juvenile shoots; the more robust size of the plants; the strong tendency for the marginal, elongate cells to be thick-walled parallel to the leaf-margins, forming a differentiated border; and the absence of any tendency to produce caducous leaves.

In the tendency of the marginal cells to form a thick-walled border (Fig. 42:9, 12) *P. diffusa* exhibits some similarity to *P. floridana,* in which the same phenomenon exists, though it is usually much less strongly exhibited. However, somewhat leptodermous phases (*Schuster* 38102) of *P. diffusa* may have this border weakly developed.

Evans (1905, p. 181) points out the close relationship of *P. smallii* to *P. diffusa* Stephani, from Cuba, from which it is supposed to differ in its greater size, lesser delicacy, narrower and longer leaves, with the margins less arched, and the longer, more spinose teeth of the perianth-mouth. Subsequently Evans (1922, p. 28) noted that the species is more widely distributed (Bahamas, Cuba) and that "Its discovery in Cuba brings up again its relationship to the Cuban *P. diffusa* Steph . . . and arouses the suspicion that the two species may be synonymous. The Cuban specimen, however, shows the distinctive

features of the species, and no connecting links between *P. smallii* and *P. diffusa* have as yet come to light."

However, I have carefully studied type material of *P. diffusa* (Cuba, *Wright*), in the New York Botanical Garden, and compared it with the type of *P. smallii*. The differences between the two seem inconsequential. The type of *P. smallii* is admittedly somewhat larger than that of *P. diffusa* (largest leaves of *smallii* supposedly to *ca.* 1000 μ wide x 3000 μ long; largest leaves of *diffusa ca.* 675-760 μ wide x 1650-1750 μ long, occasionally to 800 μ wide x 2000 μ long), but the writer cannot regard this variation in size as significant; the leaves of mature *P. diffusa* are fully 2.35-2.45 × as long as wide; in *P. smallii* supposedly to *ca.* 2.6-3.0; these differences appear correlated with size differences and again are within the range of variation to be expected. In Cuban material of *P. diffusa* the leaves of the type vary from 700 μ wide x 1650 μ long to 750 μ wide x 1750 μ long and 840 μ wide x 2000 μ long to 900 μ wide x 2100 μ long in a specimen from Banao Hills, Sta. Clara, No. 20, leg. Bro. Clement. The leaf-length varies here from 2.35-2.45 × as long as wide in almost all cases. Although the type of *P. smallii* supposedly has the leaves to 1000 x 3000 μ (*i.e.,* 3 times as long as wide), this appears to be unusual to the writer, since re-examination of the type shows that mature plants generally have the leaves only 900 μ wide x 1800-1850 μ long (*i.e.,* 2.0-2.1 × as long as wide). It is only when exceptionally robust plants are examined that the type of *P. smallii* shows leaves *ca.* 1040 μ x 2500 μ long, and I have seen no leaves that become 1000 x 3000 μ. These differences, in the writer's opinion, are subject to too much variation with size (heterogonic growth), to make them reliable for differentiating two species. *P. diffusa* is stated by Evans (1905, p. 181) to have the leaves "shorter and relatively broader, the margins more curved, the trigones of the leaf-cells are commonly indistinct, and the spine-like teeth of the mouth of the perianth are shorter." The leaves in the type plants of *P. diffusa* (NYBG) are as nearly parallel-sided as in the type of *P. smallii,* with the postical margin no more curved; the trigones are large and sometimes slightly bulging (as in the type of *smallii*); the teeth of the perianth-mouth are at most very slightly shorter. Perhaps more significant are the similarities that can be pointed out. Firstly, the type of *P. diffusa* has the leaves with the marginal 1-2 rows of cells with the walls parallel to the margins strongly thick-walled, exactly as in the type of *P. smallii.* Secondly, the collenchymatous median cells are 18-21 x 32-42 μ (23 x 37 μ in the type of *P. smallii*), the marginal cells are 15-19 x 28-34 μ (16 x 29 μ in the type of *P. smallii*); the marginal cells may be even more strongly differentiated and elongate in the type of *P. diffusa* than in *P. smallii* type, as is evident from Figure 42; in this instance, the marginal cells average 42 μ long x 14-17 μ wide; the basal median cells are 21-22 x 35-52 μ (25 x 46 μ in the type of *P. smallii*); there is therefore no significant variation in cell-size. Thirdly, the rectangular, sharply spinose female bracts in both "species" are identical.

P. diffusa may bear the perianth exactly as described for *P. smallii* "on a more or less elongated ultimate branch, usually without an innovation." Fourthly, the perianth is bilabiate in both species, campanulate, and each lip in both cases bears *ca.* 20 teeth. Fifthly, and perhaps most significantly, the two "species" have an identical facies, and totally lack any marked habitual differences. On some plants of *P. smallii* the leaves spread more widely (60-70°), but on some plants of the type they spread at only *ca.* 45-55°.

Since the preceding study was completed, I have repeatedly compared the type material, and topotypic, Floridian plants of *P. smallii* with two collections of *P. diffusa,* both labelled as from the Hepaticae Cubensis Wrightianae — hence cotypic of *P. diffusa.* The collection of this last type at the New York Botanical Garden appears inseparable from the type of *P. smallii;* the collection at Yale, however, diverges to some extent. The latter has the leaves slightly less remote, often subcontiguous when moist; it has the mature leaves more nearly obliquely spreading (*ca.* 50-55°, rather than 60-70° as in *P. smallii*); and the leaves are less narrow and less elongate, with often a lingulate-ovate shape. The gynoecia of the Yale plants are similarly variable in position as in Floridian *P. smallii*: the primary and secondary gynoecia usually bear 1-2 innovations; the gynoecia of the ultimate branches of the decompound system are commonly without innovations. The perianths in both types of plants are identical, bearing usually a narrow but entire antical wing, which is only occasionally vestigial or lacking. Although, at first glance, these differences suggest that we deal with two species, comparison of a series of plants soon obscures or obliterates most of these distinctions. The only remaining one, which impresses the writer, is the difference in leaf-orientation, brought out in the following key:

1. Leaves obliquely spreading, typically at an angle of (45) 50-55°, even on the mature parts of the shoots, typically less parallel-sided, with postical margin more arcuate, the basic leaf-shape (*in situ*) appearing to be narrowly lingulate-obovate, the leaf sometimes only *ca.* 2.0-2.2 × as long as wide. .... *P. diffusa* (typical)
1. Leaves rather widely spreading, typically slightly falcate, spreading basally at an angle of *ca.* 60-65°, but with the distal portions sometimes more widely spreading (at an angle of 75-90°), typically appearing virtually parallel-sided, *in situ,* the basic leaf-shape strap-shaped, the leaf commonly 2.2-2.5 × as long as wide. .... *P. "smallii"*

Except for the difference in orientation of the leaves, all other characters separating the two taxa appear to be quite untrustworthy. For example, the female plants (Yale herb.) of the type of *P. diffusa* from Cuba, may have the leaves sublinear and 2.5-2.8 × as long as wide! By contrast, male plants (Rangel, Taco-Taco, Pinar del Rio, Cuba, *J. Acuña* 92; Yale) have much less remote, indeed commonly contiguous, leaves that are on an average only 2.0 × as long as wide! Admittedly, in typical *P. diffusa,* the leaves, when flattened, tend to be more narrowed in their distal quarters than in *P. smallii,* but this same tendency reappears on isolated, and in particular on less mature, leaves of *P. smallii.* Equally significant, on the ultimate and penultimate branches the leaves of *P. smallii* "tend" to be as nearly suberect

or obliquely spreading as in typical *P. diffusa.* This is particularly well-marked in some plants of the type of *P. smallii.* As a consequence, I have reluctantly arrived at the conclusion that *P. smallii* cannot be maintained as a separate species. Perhaps, on the basis of the somewhat more widely spreading leaves it should be recognized as a distinct variety of *P. diffusa;* such treatment must await study of longer series of specimens than currently accessible.

In conjunction with the evaluation of the Floridian-Antillean *P. diffusa* we need to consider the plant from Ecuador assigned by Herzog (1952, p. 80, fig. 13) to *P. diffusa.* Although the habit sketches do not show marked deviation from *P. diffusa,* except in that the androecia are terminal and not intercalary (as already noted above), the leaves are shown as too nearly ovate-lingulate to correspond with any material I have seen of *P. diffusa.* I must, therefore, question the propriety of placing this material within *P. diffusa.* Certainly the leaves and bracts I have seen in both typical *P. diffusa,* and in the *P. smallii*-like phases, do not normally resemble those illustrated by Herzog.

In the abundant materials collected in Ross-Costello Hammock, Hainlin Drive, Dade Co., Florida (*Schuster* 38102, 38014), the branching patterns and occurrence of subfloral innovations were investigated in detail. The more robust plants initially develop one or two intercalary, monopodial branches, which stand at an angle of *ca.* 70-80° with the leading axis. Above this, the main axis bears *ca.* 2-4 terminal branches, equally monopodially oriented, each subtended by a narrow leaf (Fig. 41:7-8). Each, or some of these terminal branches, then undergo one or two terminal bifurcations. In some cases these pseudodichotomously oriented tertiary branches remain sterile, but often both of the terminal forks are soon floriferous, commonly after having produced only 2- to 3-pairs of vegetative leaves. The gynoecial terminal branches, in turn, may remain without an innovation, or develop a single one (which, if no perianth develops may become quite vigorous), or develop two subfloral innovations. In some cases one, of a pair of such gynoecia, develops no innovation at all, the other develops two innovations. Sometimes, however, the gynoecium occurs singly, at the apex of an elongate (usually secondary?) stem. In such cases, as noted by Evans (1905) there may be no subfloral innovation, although as is clear from Fig. 42:1, there may be a single innovation, or sometimes even two. As is evident from the preceding account, subfloral innovations are often very common in *P. diffusa,* the statement of Evans (*loc. cit.*) that the gynoecia are "usually without an innovation" hardly being a valid generalization. Evans, furthermore, attempts to use the absence of gynoecial innovations as a specific character, supposedly separating *P. smallii* (= *diffusa*) from *P. wrightii* Steph., a Cuban species. It is evident that no difference exists between the two species on this basis. The relationships between these two taxa need reinvestigation. Equally needing reinvestigation is the relationship of the present species, and *R. tenuis* Lindenb., a species supposedly differing in that the gynoecial "inflorescence bears a subfloral innovation which is itself often flori-

ferous; the leaves have fewer teeth . . . and the leaf-cells have larger and more frequently confluent trigones, which are especially conspicuous in the perianth and bracts." As we have seen, a similar occurrence of floriferous gynoecial innovations often obtains in *P. diffusa*.

Among other closely allied species is *P. jovoensis* Steph. (= *P. rutilans* var. *liebmanniana* Gottsche, 1863), judging from fig. 9g in Carl (1931), and Plate 6 in Gottsche (1863). This species appears to have a sharper antical perianth-wing, and more copiously, closely spinose-dentate bracts, as well as leaves with the postical base more longly revolute. In other respects the plants are similar in appearance. According to Herzog (1952, p. 80) *P. schinzii* Steph. is questionably conspecific with *P. diffusa;* I have not seen material of this plant.

I have searched, in vain, for any indication of asexual reproduction in the types of *P. diffusa* and of *P. smallii*. However, in the material of *P. diffusa* from Banao Hills, Sta. Clara, Cuba (leg: *Clement* 20) the undersurface of the leaves shows occasional juvenile plants developing from the leaf-cells. The asexual reproductive mechanism of this species, therefore, allies it clearly with *P. floridana* (in which Evans, 1896, mentions this type of reproduction) and with *P. ludoviciana*. It would appear that in this species, and in *P. floridana,* asexual reproduction is relatively sporadic and infrequent, compared with *P. ludoviciana*. However, in the copious collections of the writer from Ross-Costello Hammock (*Schuster* 38102, 38104) propagula are often abundantly developed, and may even be found on the postical faces of the perichaetial bracts, and develop also within the unfertilized perianths.

Experimental Trichinosis in the Golden Hamster. I. Spontaneous Muscular Activity Patterns[1]

GEORGE R. BERNARD
University of Notre Dame, Notre Dame, Indiana

In an experiment on the production of certain urinary constituents by golden hamsters (*Mesocricetus auratus*) infected with *Trichinella spiralis,* it was found (Bernard, 1954) that during the acute stages of the disease the creatinine output falls while creatine excretion rises. The latter effect was expected; the decrease in creatinine output was not. It was also observed that sick animals were less active than uninfected hamsters in adjacent metabolism cages. Could it be lack of spontaneous activity that was completely or partially responsible for the creatinine output decrease? In order to answer this question, the spontaneous activity of infected and "normal" hamsters had to be measured.

Methods

The experimental apparatus was essentially a pair of "activity analyzers" as devised by Harned *et al.,* (1952). Paired cylindrical cages of quarter-inch galvanized wire mesh, 6 inches in diameter and 11 inches high, were suspended individually by single, matched springs. Galvanized sheet metal was used for the roof of the cage. Each cage was attached to a light, counterbalanced heart lever which gave a fourfold magnification of vertical alterations of the cage's position. Only movements of the cage occupants such as walking, climbing, and gnawing were registered on the smoked surface of a slowly rotating kymograph drum. A few Purina Lab Chow pellets were placed in the cage with the animal and a 25 ml water reservoir was provided. The animals were placed in the cages at noon and the records made over a 14-hour period (6:00 PM - 8:00 AM). Hourly time signals were marked on the kymograph. The room housing the cages was darkened and no one entered it during the recording period. The temperature range of the room was that of the building: 18-24°C.

First, the normal diel activity (Carpenter, 1935) of six normal littermate male hamsters was recorded. Males were used in order to avoid any possible cyclical effects of estrus (Hemmingsen and Krarup, 1937). Four of the animals were infected when they were 12 weeks

[1] Some of the observations reported here were made while the author was a Public Health Service Research Fellow of the National Microbiological Institute and were submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Boston University. The author is indebted to Dr. Arthur G. Humes for guidance and encouragement.

old. Each received through a stomach tube a dose of 225 *Trichinella* larvae which had been isolated from rat muscle by digestion in a pepsin-hydrochloric acid mixture using the method of Larsh and Kent (1949). Because the experimental apparatus had but a pair of cages, only two hamsters, "control" and "infected", could be observed at one time. Each of the four infected hamsters was paired with one of the two uninfected animals. Each animal was assigned a particular activity cage for the duration of the experiment; activity records were made with paired individuals occupying their assigned cages.

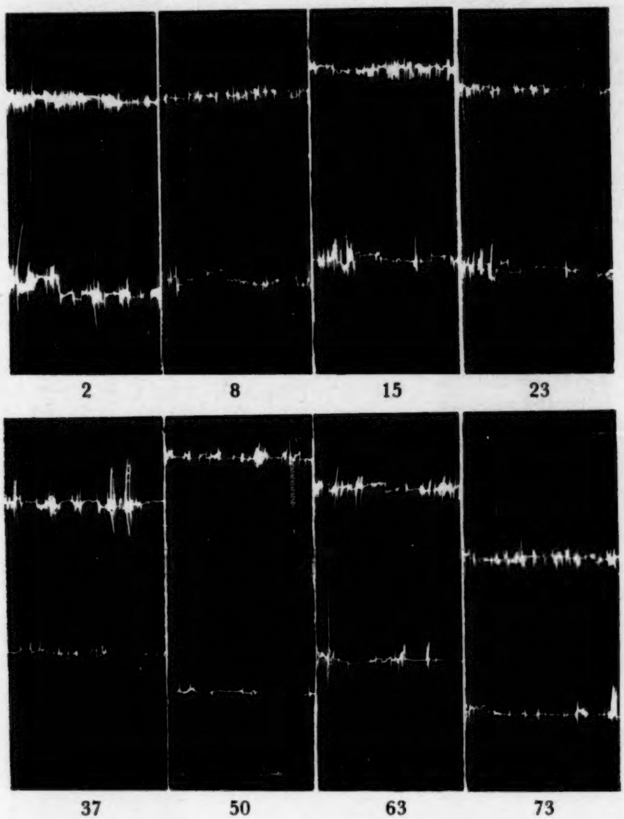

Fig. 1.—Activity records of one pair of animals. Upper line on each record is the "normal activity"; the lower line was made by the movements of the littermate *Trichinella*-infected hamster. The subscript numbers refer to days *p.i.* Each record represents the 8:40-10:40 P.M. interval.

RESULTS

The activity patterns of all six animals before the start of the experiment were similar. Figure 1 is a composite of kymographic records of one pair of animals taken on various days *post infectionem* (*p.i.*). The separate daily records are of a two-hour period (8:40-10:40 PM, E.S.T.). This time interval was found to be the longest and most active period of this nocturnal animal under laboratory conditions. During the evening hours much of the activity takes the form of gnawing at the food or cage, climbing the wall and either scrambling or dropping to the floor, and tidying the floor by moving the food pellets. In the activity analyzer the falls to the floor would register as large sweeps of the writing lever.

Because of variability in the animals themselves (e.g., decreasing weights of infected animals) it is difficult to quantitate the amount of activity in such an apparatus. Temporal relationships in the parasite's cycle and the host's response also vary slightly. However, certain distinct changes in the activity patterns of infected hamsters were noted. The activity of infected hamsters decreased about 5-7 days *p.i.* (Fig. 2). This period coincides with the period of destruction of the intestinal tissue by the adult worms (Gould, 1945; Boyd and Huston, 1952 and 1954; Humes and Akers, 1952). During the

Fig. 2.—Activity record of an infected (upper line) and "normal" littermate hamster (lower line) five days *p.i.* Note the lack of activity in this infected animal. This change lasted only one day in this animal.

Fig. 3.—Activity records of a "normal" (upper line) and littermate infected hamster ten day *p.i.* Note the apparent hyperactivity of the infected hamster.

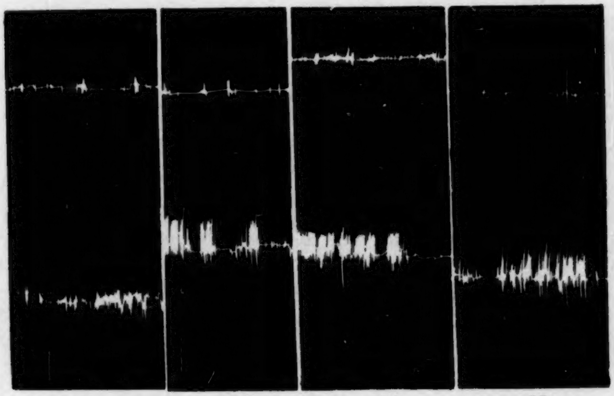

Fig. 4.—Activity records of an infected hamster which died during the experiment (upper line) and littermate normal hamster. The numbers refer to the days *p.i.*

following two weeks infected hamsters showed normal activity or were slightly hyperactive. Most of the records show an unusual amount of climbing and dropping to the floor during this period (Fig. 3). Normal hamsters, it should be noted, may have climbed just as much, but by scrambling down the activity would appear less dramatically on the record. Activity of the infected animals practically ceased about day 30 *p.i.* and did not return to the normal range until the 10th week *p.i.* at which time the observations were stopped. The infected animal whose records appear in Figure 1 shows this return of activity.

One of the infected hamsters died on day 29 *p.i.* Figure 4 shows that the animal was severely affected by the presence of the parasite. Several hours before death the animal had been lightly anaesthetized with Nembutal (pentobarbital sodium) in order that an electrocardiogram could be taken. The EKG revealed a 2:1 atrioventricular block; this might indicate the appearance of the larval worms in the myocardium. Previous electrocardiograms of this animal taken before infection and on days 5, 12, and 19 *p.i.* were normal. Death of the animal is attributed to circulatory failure.

DISCUSSION

Since the pioneering work of Slonaker (1907) and Szymanski (1918), many investigators have studied the spontaneous activity of rodents, especially the laboratory rat. The usual experiments involve studies of environmental alterations or the pharmacodynamic action of drugs. As far as can be determined, studies of the activity pattern

of mammals with trichinosis (or any other disease affecting the muscular system) have not been heretofore reported.

Interpretation of the kymographic records requires consideration of two factors: the life cycle stages of the parasite, and the pathological alterations in the affected muscle fibers. It has been established by Humes and Akers (1952) [working in the same laboratory on the same hamster colony but with a larger initial dose (approximately 1000 larvae)] that *Trichinella* larvae are in the peripheral blood stream of the golden hamster during the period from 3 to 22 days *p.i.* (Since the last living adult was observed by them on day 27, and a single dead female on day 34, larvae are probably not produced in any quantity after the 4th week *p.i.*) Presumably during this time the larvae are penetrating the muscle fibers, although larvae were not found in the cheek pouch muscle fibers (and diaphragm) until the 16th day. It is assumed that the appendicular muscles are infected simultaneously. The point to be considered is that most of the larvae have penetrated into the muscle fibers and have long been resident there before inactivity on the part of the host develops.

Pathological changes of the invaded muscle fiber in experimental and clinical trichinosis are summarized and discussed by Gould (1945). With invasion by the trichinae, there is: 1) proliferation of muscle nuclei; 2) basophilic granular, hyaline, and hydropic degeneration of muscle fibers; and 3) capillary proliferation, hyperemia, and edema. There follows an infiltration of neutrophilic and eosinophilic polymorphonuclear leucocytes, lymphocytes, and tissue histiocytes. The inflammatory reaction is greatest during the 5th or 6th week *p.i.*, at the time when the permanent capsules form. Observations (unpublished) on infected tongue muscles of the hamster agree in most details with this description. Plasma cells have also been reported in the vicinity of the larvae. The present author has not noted extraordinary numbers of these distinctive cells, but rather large numbers of histiocytes with eosinophil granules, the eosinocytes of Bessis (1956), were observed in the connective tissue of the muscle. Hematological evidence that the inflammatory reaction subsides by the 10th week *p.i.* is presented by Bernard (1954).

The period of inactivity which commences about 30 days *p.i.* is probably a result of the local inflammatory reaction about, and the destruction and necrosis of the affected muscle fibers. The apparent hyperactivity which precedes this phase (cf. Fig. 2) may actually be caused by asthenia, hypersensitivity, or both. The animal climbs, becomes fatigued or suffers muscular pain, and drops to the floor. The observations (*in vivo*) of Humes and Akers (1952) established that muscular striations disappear in the invaded muscle fiber on the 19th day. Excluding other factors such as respiration, circulatory capacity, metabolic alterations, etc., a muscle with an increasing number of such minute lesions would become progressively weaker. The running ability of rats 6-7 weeks *p.i.* was studied by von Brand *et al.* (1954) and found to be reduced to 20 percent of the control

value. Rats with 2-3 -week-old infections also showed reductions, but they were not as large. Long term deleterious effects on the working ability of some infected rats were also observed. In the hamster there seems to be no long term effect on spontaneous activity although the capacity for work might be affected.

SUMMARY

The golden hamster is a nocturnal animal with the major period of activity during the interval 8:00-11:00 PM.

The spontaneous activity of hamsters is altered following infection with *Trichinella*. During the reinvasion of the intestinal mucosa by the adult worms (days 5-7 *p.i.*) activity is reduced. There follows a two-week period of normal to slightly above normal activity. Between the 4th and 9th weeks activitity is sharply curtailed. In an animal which died of the infection, activity was subnormal throughout the course of the disease.

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Studies on the Thyasinae of North America
(Acarina: Hydryphantidae)[1]

DAVID R. COOK
Wayne State University, Detroit, Michigan

The present work deals with the 17 species belonging to the subfamily Thyasinae known to occur in North America. Since there are still large areas of North America which have been poorly collected for water mites, this list is without doubt incomplete. There are several thyasin genera, with a widespread palearctic distribution, which are as yet unreported from this continent. Because so many water mite genera, formerly known only from the Old World, have been collected in North America during the last few years, it seems probable that members of some or all of these European thyasin genera may be taken in future collections.

Compared to many other groups of Hydracarina, the Thyasinae have received little attention in North America. The first records from this continent were three species described under the generic name *Thyas* by Koenike (1895). Two of these species were later placed in other genera. Mitchell (1953) in his treatment of the family Hydryphantidae gave a detailed account of the early work on the subfamily Thyasinae. Cook (1953, 1955) described two new thyasin genera, one of which is now considered by the author to be only a subgenus. Habeeb (1954) erected a new genus and five new species based on specimens from eastern United States and Canada. The new genus and three of the new species are considered synonyms by the present author. Habeeb (1958) also described a new species of *Thyasides* from New Brunswick.

The presence or absence of pigment in the median eye has been considered to be of strong phylogenetic significance and in some classifications the forms with pigmented median eyes have been placed in a separate subfamily Euthyasinae. For reasons which will be given during the discussion of the *Panisopsis*-complex, the author feels that the median eye character alone is of little taxonomic value, and at best should be used to separate subgenera.

Members of the subfamily Thyasinae often exhibit much intraspecific variation, even within a single population. As would be expected, populations of the same species from widely scattered localities show certain differences. However, in view of the extremes of variation often found in members of a species within a given area, it is felt that little would be gained by giving these populations a trinomial name. Likewise, when it can be shown that specimens of our North

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[1] Contribution No. 28 from the Department of Biology, Wayne State University.

American species fall within the limits of variation of the European species, they are considered to be identical.

With the exception of *Trichothyas musicola* (Mitchell), *Panisopsis asopos* (Cook), and *Thyopsella dictyophora* Cook, whose descriptions have appeared in recent, easily accessible journals, all species are illustrated and redescribed. No attempt has been made to present a complete synonymy of the holarctic species. In most cases only the synonymy involving published records of North American specimens has been given.

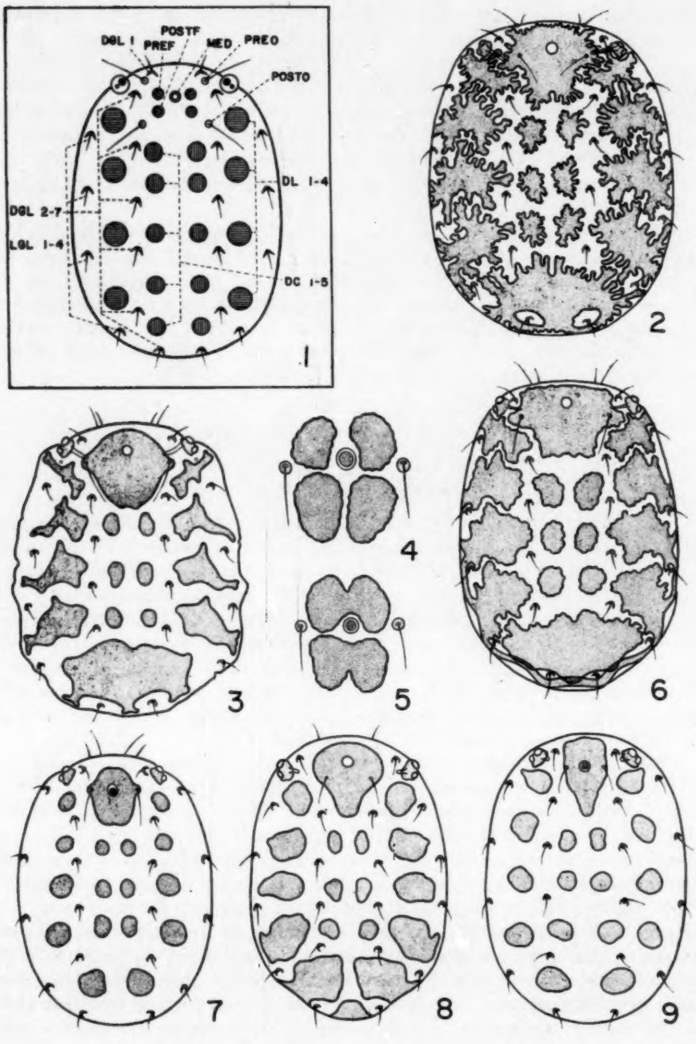
Appreciation is extended to the following people for their aid during the course of this study: To Rodger D. Mitchell for the generous loan of slide material and helpful suggestions; to O. Lundblad for his kindness in comparing several of our thyasins with European species; to Karl Viets for the gift of specimens of European Thyasinae; and to Herbert Habeeb for the loan of slides of the specimens which he described from eastern North America (Habeeb, 1954).

Subfamily THYASINAE Viets

Thyasinae Viets 1926. Zool. Anz. 69:190.
Euthyasinae Viets 1931. *Ibid.* 93:210.

Subfamily diagnosis.—Color red, integument papillate; dorsum with a series of sclerotized plates, these variously expanded and fused; median eye with or without pigment; lateral eyes usually in capsules; legs without swimming hairs, claws simple; dorsodistal portion of P-IV extending beyond the insertion of P-V, forming a chelate palp; genital flaps present, although these sometimes reduced to immovable sclerites; typically with three pairs of genital acetabula, occasionally polyacetabulate. In general, the Thyasinae are residents of temporary ponds, bogs, springs, streams, and seepage areas. They are almost never found in permanent standing waters.

One of the primary characters upon which the systematics of the Thyasinae has been based is the size and fusion of the dorsal plates. Fig. 1 shows a schematic representation of the basic dorsal sclerites as given by Lundblad (1927). Of our North American species, only *Thyas pachystoma inepta* Lundblad (Fig. 10) fits this generalized condition exactly. All other species show varying degrees of fusion of these plates. The basic pattern of the dorsum is as follows: (1) a pair of pre- and postfrontalia, which are sclerites in the region of the median eye; these plates are often fused and enlarged to form a large frontal plate (ocular plate) which surrounds the median eye. (2) five pairs of dorsocentralia, which are sclerites located slightly to either side of the midline; the first pair of these dorsocentralia are often fused with the frontal plate. (3) four pairs of dorsolateralia, which are sclerites lying laterad to the dorsocentralia. (4) a pair of pre- and postocularia, which are long, thin setae which lack associated glands; the postocularia are sometimes incorporated into the frontal plate. (5) four longitudinal rows of setae-bearing glands; the two rows nearest the



Figs. 1-9. — 1. Schematic drawing of the dorsum of a hypothetical thyasin (after Lundblad) Dc. 1-5, dorsocentralia 1-5; Dgl. 1, dorsoglandularia 1; Dgl. 2-7, dorsoglandularia 2-7; Dl. 1-4, dorsolateralia 1-4; Lgl. 1-4, lateroglandularia 1-4; Med., median eye; Pref., prefrontalia; Preo., preocularia; Postf., postfrontalia; Posto., postocularia. 2. ***Panisus cataphractus,*** dorsal view, female. 3. ***Panisus cataphractus,*** dorsal view, female. 4. ***Panisopsis gorhami,*** median eye re-

midline are called dorsoglandularia, the two rows nearest the lateral margins are called lateroglandularia. Since various degrees of fusion of the dorsal sclerites may be found within a single population of a species, a certain amount of care must be exercised when using this character alone for the establishment of genera or species. A more natural classification may be derived if morphology of the dorsal sclerites is used in conjunction with other characters, such as the structure of the genital field, coxae, and the appendages. The sexes are usually very similar, but the female always differs from the male in its possession of a pregenital sclerite.

Genus THYAS Koch

Thyas Koch 1836. Deutschl. Crust., Myr., Arach. Heft 5, no. 18.

Genotype.—*Thyas venusta* Koch. (This species cannot be recognized with certainty. Lundblad (1927) feels that *T. venusta* may be *T. barbigera* Viets).

Generic diagnosis.—Pre- and postfrontalia separate or fused on their respective sides, never fused medially to form a frontal plate; median eye with or without pigment; pigment when present diffuse; dorsocentralia 1 and 2 usually fused, but separate in one species; all dorsal sclerites relatively small; three pairs of genital acetabula, second pair of acetabula much closer to third pair than to first pair; genital flaps not extending beyond first acetabula.

Subgenus THYAS Koch

Subgeneric diagnosis.—Characteristics of the genus, except median eye does not contain pigment.

THYAS (THYAS) BARBIGERA Viets

Figs. 16, 17, 35, 57.

? *Thyas venusta* Koch 1836. Deutschl. Crust., Myr., Arach. Heft 5.
T. barbigera Viets 1908. Zool. Anz. 33:670.
T. stolli Habeeb 1954. Leaflets Acadian Biol. no. 2: 2.

Male.—Length of body 1170μ-1530μ; pre- and postfrontalia usually fused on their respective sides (Fig. 16), although they may sometimes be separate on one or both sides; median eye without pigment, lying free in integument; dorsocentralia 1 and 2 fused on their respective sides; genital field 244μ-279μ in length; with a row of short setae along median edge of genital flaps (Fig. 17), remainder of flaps without setae; second and third pairs of genital acetabula fused into a common sclerite at their bases; dorsal lengths of palpal segments, P-I, 54μ-64μ; P-II, 106μ-122μ; P-III, 84μ-98μ; P-IV, 176μ-195μ; P-V,

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gion, female. 5. ***Panisopsis gorhami,*** median eye region, female. 6. ***Panisus condensatus,*** dorsal view, female. 7. ***Panisopsis gorhami,*** dorsal view, male. 8. ***Panisopsis setipes,*** dorsal view, male. 9. ***Panisopsis pedunculata,*** dorsal view, female.

35μ-42μ. Fig. 57 shows chaetotaxy of palp. Dorsal lengths of segments of second leg, II-Leg-1, 66μ-80μ; II-Leg-2, 104μ-121μ; II-Leg-3, 136μ-164μ; II-Leg-4, 209μ-261μ; II-Leg-5, 263μ-331μ; II-Leg-6, 285μ-349μ. Figure 35 shows chaetotaxy of end segments of second leg.

Female.—Similar to male except that it possesses a pregenital sclerite.

Range.—Holarctic; the author has collected *T. barbigera* in Maryland, Michigan, and Minnesota. A slide of a specimen identified by Habeeb (1954) as *T. stolli* was examined and found to be *barbigera.* If all of Habeeb's determinations of *stolli* are likewise in error, it would increase the known range of *T. barbigera* to include Maine, New Jersey, and New Brunswick.

Habitat.—Temporary ponds.

Remarks.—Dr. O. Lundblad kindly compared specimens of *T. barbigera* from Michigan with those from Europe and stated that he could find no significant differences. *T. barbigera* may be separated from all other North American members of the genus *Thyas* by the following characters: median eye without pigment; bases of second and third genital acetabula located on a common sclerite, this sclerite with a few setae posteriorly; second pair of genital acetabula located anterio-medial to third pair; legs relatively long and slender.

THYAS (THYAS) STOLLI Koenike

Figs. 13, 14, 23, 24, 38, 54.

Thyas stolli Koenike 1896. Abhandl. naturw. Ver. Bremen, 13:194.
T. stolli Koenike 1912. Trans. Roy. Canadian Inst. 1912:288.
T. stolli Mitchell 1953. Amer. Midland Nat. 49:160.
T. stolli Mitchell 1954. Fieldiana: Zool. 35:36.
T. tobiquensis Habeeb 1954. Leaflets Acadian Biol. no. 2:2
(new synonymy) non *T. stolli* Habeeb 1954. *Ibid.* no. 2:2.

Male.—Length of body 810μ-990μ; pre- and postfrontalia either separate or fused on their respective sides, occasionally fused on one side and separate on other (Fig. 23); median eye without pigment, lying free in integument; dorsocentralia 1 and 2 fused on their respective sides; genital field 196μ-227μ in length; with a row of setae along median edge of genital flaps (Fig. 14), remainder of flaps without setae; second and third pairs of genital acetabula fused into a common sclerite at their bases; dorsal lengths of palpal segments: P-I, 42μ-56μ; P-II, 82μ-101μ; P-III, 56μ-70μ; P-IV, 136μ-166μ; P-V, 31μ-36μ. Figure 54 shows chaetotaxy of palp. Dorsal lengths of segments of second leg: II-Leg-1, 56μ-72μ; II-Leg-2, 68μ-91μ; II-Leg-3, 86μ-118μ; II-Leg-4, 128μ-180μ; II-Leg-5, 168μ-224μ; II-Leg-6, 176μ-219μ. Figure 38 shows chaetotaxy of distal segments of second leg.

Female.—Similar to male in most measurements; body somewhat larger, with specimens reaching a length of 1100μ; greatest difference lies in the rather pronounced dimorphism (for a *Thyas*) of the genital field (Fig. 13); length of genital field 229μ-284μ.

Range.—Known from Michigan, British Columbia, and New Brunswick.

Habitat.—Temporary ponds.

Remarks.—*T. stolli* may be separated from other North American species of *Thyas* by the following combination of characters: median eye without pigment; bases of second and third genital acetabula on a common sclerite, this sclerite with a few setae posteriorly; second pair of genital acetabula located medial to third pair; legs relatively short. During the spring of 1951, several *T. stolli* females were isolated in small vials and egg masses were obtained. The immature stages coming from these eggs varied in that mites emerged from some egg masses as larvae, from other egg masses as nymphs. No differences were found in the morphology of the females which could be correlated with the difference in life history. The European species, *T. dirempta* Koenike, is very closely related to *T. stolli* and may actually be only a subspecies of *stolli.*

THYAS (THYAS) PACHYSTOMA INEPTA Lundblad
Figs. 10, 18, 39

Thyas inepta Lundblad 1925. Ent. Tidskr. 46:177.
T. pachystoma inepta Lundblad 1927. Zool. Bidrag. Uppsala 11:263.

Female.—(based on a single specimen) Length of body 1620μ; pre- and postfrontalia separate; median eye without pigment, lying free in integument; median eye surrounded by a relatively small sclerotized ring; dorsocentralia 1 and 2 separate; genital field 323μ in length; second pair of genital acetabula located anterior to third pair; second and third acetabula not fused into a common sclerite at their bases (Fig. 18); pregenital sclerite and vulvular sclerite fused; dorsal lengths of palpal segments: P-II, 124μ; P-III, 92μ; P-IV, 212μ; P-V, 42μ; dorsal lengths of segments of second leg: II-Leg-1, 98μ; II-Leg-2, 116μ; II-Leg-3, 162μ; II-Leg-4, 279μ; II-Leg-5, 315μ; II-Leg-6, 340μ. Figure 39 illustrates chaetotaxy of distal segments of second leg.

Range.—Holarctic; the North American record of *T. pachystoma inepta* is from Alaska.

Habitat.—Temporary pools in the tundra.

Remarks.—*T. pachystoma inepta* may be separated from other North American species of *Thyas* by the following characters: bases of second and third genital acetabula not fused into a common sclerite; pre- and postfrontalia, dorsocentralia 1 and 2 all separate; legs relatively long. Habeeb (1954) reports *Thyas pachystoma* Koenike from a bog in New Jersey.

THYAS (THYAS) RIVALIS Koenike
Figs. 12, 15, 34, 62

Thyas rivalis Koenike 1912. Zool. Anz. 40:63.

Female.—Length of body 967μ-1485μ; pre- and postfrontalia fused into plates similar in size and shape to dorsocentralia (Fig. 12); me-

dian eye without pigment; median eye lying free in integument; median eye surrounded by a relatively large sclerotized ring; dorsocentralia 1 and 2 usually separate, but occasionally fused on their respective sides; genital field 226μ-318μ in length, with a row of setae along median edge of genital flaps (Fig. 15); second pair of acetabula located anterior to third pair; second and third acetabula not fused into a common sclerite at their bases; dorsal lengths of palpal segments: P-I, 52μ-64μ P-II, 94μ-112μ; P-III, 56μ-68μ; P-IV, 144μ-180μ; P-V, 38μ-46μ. Figure 62 shows chaetotaxy of palp. Dorsal lengths of segments of second leg: II-Leg-1, 64μ-80μ; II-Leg-2, 76μ-108μ; II-Leg-3, 104μ-140μ; II-Leg-4, 154μ-212μ; II-Leg-5, 164μ-232μ; II-Leg-6, 204μ-236μ. Figure 34 illustrates end segments of second leg.

Range.—Holarctic; in North America, specimens of *T. rivalis* have been collected in Michigan and Minnesota.

Habitat.—All of the New World specimens have come from small, slowly-flowing streams.

Remarks.—The present species may be separated from other North American members of its genus as follows: bases of second and third genital acetabula not fused into a common sclerite; pre- and postfrontalia fused into plates resembling the dorsocentralia; legs relatively short and stocky. In contrast to most other species of the genus, *T. rivalis* is an inhabitant of streams rather than temporary ponds.

Subgenus ZSCHOKKEA Koenike

Zschokkea Koenike 1892. Zool. Anz. 15:230.

Subgenotype.—*Zschokkea oblonga* Koenike.

Subgeneric diagnosis.—Characteristics of the genus except that median eye contains pigment.

THYAS (ZSCHOKKEA) BRUZELII Lundblad

Figs. 11, 19, 22, 27, 31, 51

Thyas bruzelli Lundblad 1926. Ent. Tidskr. 47:205.

T. mainensis Habeeb 1954. Leaflets Acadian Biol. no. 2:2 (new synonymy).

Male.—Length of body 1124μ-1665μ; pre- and postfrontalia separate; median eye containing a variable amount of pigment; occasionally amount of pigment in median eye so reduced as to appear, or actually be, absent; dorsocentralia 1 and 2 fused on their respective sides; genital field 228μ-340μ in length; with a row of setae on median edge of genital flaps and numerous scattered setae over general surface of flaps (Fig. 11); second and third pairs of genital acetabula fused into a common sclerite at their bases, with numerous setae along medio-posterior edge of this sclerite; second pair of genital acetabula lying medial to third pair; capitulum relatively long and slender (Fig. 27), length 279μ-436μ; dorsal lengths of palpal segments: P-I, 54μ-80μ; P-II, 112μ-165μ; P-III, 72μ-116μ; P-IV, 188μ-261μ; P-V, 36μ-52μ. Figure 51 shows chaetotaxy of palp. Dorsal lengths of seg-

ments of second leg: II-Leg-1, 72μ-99μ; II-Leg-2, 80μ-132μ; II-Leg-3, 122μ-172μ; II-Leg-4, 190μ-305μ; II-Leg-5, 236μ-383μ; II-Leg-6, 235μ-349μ. Figure 31 shows end segments of second leg.

Female.—Similar to male except that it possesses fewer setae on the surface of the genital flaps (Fig. 19), averages slightly larger, and has a pregenital sclerite.

Range.—Holarctic; this species is known from Michigan, Maine and Sweden.

Habitat.—Temporary ponds.

Remarks: *T. bruzelii* may be easily separated from other nearctic species of *Thyas* by its possession of a pigmented median eye. The genital field also differs in that there are numerous setae along the medio-posterior edge of the sclerite at the bases of the second and third acetabula. The amount of pigment in the median eye varies considerably, even within a single population. Usually there is a moderate amount of pigment present, but in some specimens the pigment was greatly reduced and in two or three instances appeared to actually be absent. Lundblad (1926) did not report pigment in the median eye of *bruzelii*. A specimen of *bruzelii* from Michigan was sent to Dr. Lundblad for comparison with the holotype. He stated that he could find no appreciable difference between the two mites. Habeeb (1954) described a male specimen of *bruzelii* under the name *T. mainensis*. Although no mention of it was made in the original description, an examination of the slide preparation of *mainensis* disclosed the presence of pigment in the median eye.

Genus THYASIDES Lundblad

Thyasides Lundblad 1926. Ent. Tidskr. 47:208.

Genotype.—*Thyasides dentata* (Thor).

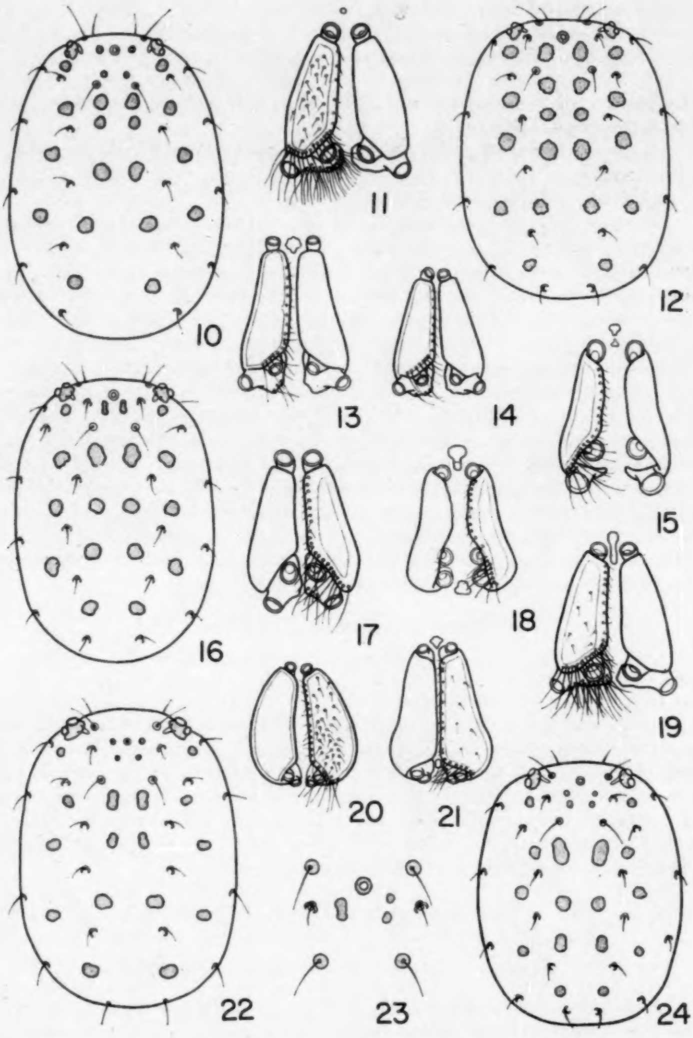
Generic diagnosis.—Pre- and postfrontalia typically fused to form a small frontal plate surrounding median eye; occasionally pre- and postfrontalia fused on their respective sides only, leaving median eye free in integument (similar to *Thyas*); median eye with two small dots of pigment; dorsocentralia 1 and 2 fused on their respective sides; dorsal plates relatively small; with three pairs of genital acetabula, second and third pairs nearly touching each other.

THYASIDES SPHAGNORUM Habeeb

Figs. 20, 21, 25, 26, 32

Thyasides sphagnorum Habeeb 1958. Leaflets Acadian Biol. no. 17.1.

Male.—Length of body 900μ-1080μ; pre- and postfrontalia usually fused into a small, lobed frontal plate which surrounds median eye (Fig. 25); occasionally pre- and postfrontalia fused on their respective sides only, leaving median eye free in integument and giving mite a superficial resemblance to a member of the genus *Thyas* (Fig. 26); median eye with pigment in form of two small dots; dorsocentralia 1 and 2 fused on their respective sides; genital field 226μ-253μ in length; second and third acetabula very close together (Fig. 20);



Figs. 10-24. — 10. *Thyas pachystoma inepta*, dorsal view, female. 11. *Thyas bruzelii*, genital field, male. 12. *Thyas rivalis*, dorsal view, female. 13. *Thyas stolli*, genital field, female. 14. *Thyas stolli*, genital field, male. 15. *Thyas rivalis*, genital field, female. 16. *Thyas barbigera*, dorsal view, male. 17. *Thyas barbigera*, genital field, male. 18. *Thyas pachystoma inepta*, genital field, fe-

genital flaps covered with numerous short setae on general surface, with 5-8 longer setae at posterior edge of flaps; dorsal lengths of palpal segments: P-I, 47μ-51μ; P-II, 88μ-104μ; P-III, 67μ-74μ; P-IV, 144μ-161μ; P-V, 30μ-36μ. Figure 32 shows chaetotaxy of palp. Dorsal lengths of segments of second leg: II-Leg-1, 64μ-72μ; II-Leg-2, 79μ-88μ; II-Leg-3, 96μ-112μ; II-Leg-4, 172μ-188μ; II-Leg-5, 209μ-235μ; II-Leg-6, 226μ-262μ.

Female.—Similar to male except it averages larger, possesses a genital field which is proportionally narrower and has fewer setae on general surface of flaps (Fig. 21); with 5-7 longer setae on posterior edge of genital flaps.

Range: *T. sphagnorum* has been collected in New Brunswick and both peninsulas of Michigan.

Habitat.—Temporary waters, especially those associated with bogs.

Remarks.—Identification of *T. sphagnorum* presents no problem in those individuals with the pre- and postfrontalia fused into a frontal plate. However, specimens in which the frontalia remain separate could be confused with *Thyas,* especially if the pigment in the median eye is destroyed during slide making. In the latter case the structure of the genital field, with the second and third acetabula being very close together, should serve for identification. *T. sphagnorum* closely resembles the European species, *T. dentata* but differs in that it possesses approximately half the number of long setae at the posterior end of the genital flaps. The drawing of the female genital field of *dentata* by Lundblad (1927) shows 12 of these setae on one side and 14 on the other. Also, there is a strong tendency for the pre- and postfrontalia to remain unfused medially in the North American species. The author has no knowledge of such an occurrence in the European species, but Lundblad (1925) described *T. dentata separata,* based on a specimen in which the pre- and postfrontalia were fused medially, but did not enclose the median eye.

Genus EUTHYAS Piersig

Euthyas Piersig 1898. Zool. Anz. 21:575.

Genotype.—Euthyas truncata (Neuman).

Generic diagnosis.—Pre- and postfrontalia fused to form a spindle-shaped frontal plate which surrounds the pigmented median eye; pigment of median eye grouped into two small dots; papillae of integument forming small rosettes; capitulum long and narrow; dorsocentralia 1 and 2 fused on their respective sides; three pairs of genital acetabula, these relatively small; second pair of acetabula located midway between first and third pairs.

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male. 19. *Thyas bruzelii,* genital field, female. 20. *Thyasides sphagnorum,* genital field, male. 21. *Thyasides sphagnorum,* genital field, female. 22. *Thyas bruzelii,* dorsal view, male. 23. *Thyas stolli,* median eye region, male. 24. *Thyas stolli,* dorsal view, male.

EUTHYAS TRUNCATA (Neuman)
Figs. 28, 29, 44, 46

Bradybates truncatus Neuman 1874. Skand. Naturforsk. Kopenhamn Forhandl. 1873:409.
Euthyas Wardi Habeeb 1954. Leaflets Acadian Biol. no. 2:3 (new synonymy).

Male.—Length of body 1305μ-1620μ; pre- and postfrontalia fused into a somewhat spindle-shaped frontal plate 144μ-208μ in length, 72μ-88μ in greatest width; median eye with two small dots of pigment; dorsocentralia 1 and 2 fused to form narrow plates 80μ-116μ in length; genital acetabula small, second pair located approximately midway between first and third pairs; genital field oval in outline (Fig. 44), 314μ-266μ in length; genital flaps bearing numerous setae; capitulum very long and narrow (Fig. 28), 471μ-558μ in length; dorsal lengths of palpal segments: P-I, 44μ-54μ; P-II, 152μ-164μ; P-III, 112μ-121μ; P-IV, 192μ-224μ; P-V, 40μ-48μ. Figure 46 shows chaetotaxy of palp. Dorsal lengths of segments of second leg: II-Leg-1, 88μ-92μ; II-Leg-2, 180μ-201μ; II-Leg-3, 176μ-196μ; II-Leg-4, 252μ-279μ; II-Leg-5, 345μ-366μ; II-Leg-6, 293μ-321μ; papillae of integument arranged in the form of small rosettes.

Female.—Similar to male except that it averages slightly larger, has a pregenital sclerite, and possesses fewer setae on the genital flaps.

Range.—Holarctic; in North America *E. truncata* has been collected in Michigan and New Jersey.

Habitat.—Temporary ponds.

Remarks.—Dr. Lundblad compared specimens of *E. truncata* from Michigan with those from Europe and found them to be almost identical. The fact that both *Thyasides* and *Euthyas* have the pre- and postfrontalia fused into a frontal plate surrounding a median eye containing pigment in the form of two small dots, has led some workers to the conclusion that they are closely related genera. However, the structure of the frontal plate, genital field, and integument is much different in the two genera. *Thyasides* much more closely resembles *Thyas* in structure of the genital field and dorsal plates, especially when the pre- and postfrontalia fail to fuse into a frontal plate. The main similarity between *Euthyas* and *Thyasides* is median eye pigment in the form of two dots, and median eye pigment is known to be variable in the thyasins. The present author feels that *Thyasides* is much more closely related to *Thyas* than to *Euthyas.*

The PANISOPSIS Complex

Under some classifications of the *Thyas*-like mites (for example, Viets, 1936) the presence or absence of median eye pigmentation separates the subfamilies Thyasinae and Euthyasinae. In such a classification, groups like *Zschokkea* and *Panisopsis,* which possess a pigmented median eye, are put in the Euthyasinae, while *Thyas* and *Panisoides,* which lack pigment in the median eye, are placed in the Thyasinae. The least specialized of the thyasin groups, exhibiting a

minimum of fusion of the dorsal sclerites, are *Thyas* and *Zschokkea* which are usually considered to resemble the ancestral thyasin type. Except for the median eye character, *Thyas* and *Zschokkea* are almost identical morphologically (compare Figs. 14 and 24) of *Thyas* (*Thyas*) *stolli* with Figs. 19 and 22 of *Thyas* (*Zschokkea*) *bruzelii*). If the Thyasinae and Euthyasinae represent valid phyletic lines, they must have evolved separately from generalized forms similar to *Thyas* and *Zschokkea*. It seems extremely improbable that independent evolution along each line could have produced groups as similar as *Panisopsis* (with a pigmented median eye) and *Panisoides* (without a pigmented median eye). A comparison of the genital fields (Figs. 41, 37), legs (Figs. 63, 55), and dorsal plates (Figs. 9, 8) of *Panisopsis pedunculata* and *Panisoides setipes* will show their striking similarities. Other indications in favor of a theory that pigment may have appeared or disappeared more than once in thyasin evolution are to be found in the following observations. The author has collected populations of both *Panisopsis (Panisopsis) gorhami* and *Thyas (Zschokkea) bruzelii* in which the concentration of median eye pigment varied from a large amount to almost none. This is evidence of the variability of the pigment and strongly suggests that pigment may become reduced and disappear. If pigment in the median eye has disappeared twice or even several times during thyasin evolution, it is a poor character upon which to base phylogeny. Therefore, Euthyasinae is placed as a synonym of Thyasinae and the median eye character alone, unless backed up by other differences, is considered the basis of subgeneric splitting only.

Of the four generic names which have previously been proposed for members of the *Panisopsis*-complex, *Panisopsis, Panisoides, Marshallothyas,* and *Acadiothyas, Panisopsis* is the oldest and is retained as the generic name. The subgenus *Panisopsis* includes those forms with a pigmented median eye. *Acadiothyas,* which also has a pigmented median eye, was described from a single specimen having three separate plates in the median eye region rather than the single large plate typical of most species of *Panisopsis.* Western populations of *Acadiothyas* exhibit much variation in the frontal plates. In a single population, specimens may be found with four, three, two, or one frontal plate (Figs. 4, 5, 7). Because the characters of *Acadiothyas* grade into those of *Panisopsis,* it is considered to be a synonym of the latter. In the forms without a pigmented median eye, *Panisoides* and *Marshallothyas,* the frontal plate characters do not grade into each other, and they are retained as separate subgenera.

Genus PANISOPSIS Viets

Panisopsis Viets 1926. Zool. Anz. 66:145.
Panisoides Lundblad 1926. Ent. Tidskr. 47:208.
Marshallothyas Cook 1953. Proc. Ent. Soc. Wash. 55:305.
Acadiothyas Habeeb 1954. Leaflets Acadian Biol. no. 2:2.

Genotype.—*Panisopsis vigilans* (Piersig).

Generic diagnosis.—Pre- and postfrontalia, dorsocentralia 1 and the postocularia fused into a large frontal plate in most species, but exhibiting variable fusion in some; there is a tendency towards expansion of the dorsocentralia and dorsolateralia, but in some species these are no larger than those found in *Thyas;* median eye with or without pigment; lateral eyes in capsules; three pairs of genital acetabula; genital flaps with setae located anterior to first pair of acetabula; width of genital flaps greatly reduced near posterior end.

Subgenus Panisopsis Viets

Subgeneric diagnosis.—Characteristics of the genus, except that the median eye contains pigment, although amount of pigment sometimes greatly reduced.

Panisopsis (Panisopsis) gorhami (Habeeb)

Figs. 4, 5, 7, 42, 49, 53

Acadiothyas Gorhami Habeeb 1954. Leaflets Acadian Biol. no. 2:2.

The following descriptions are based on specimens collected by Rodger Mitchell from a spring in Lamoille County, Vermont. Since the original description was based on a female mite from New Brunswick, it seems best to discuss the eastern population first. Only females were present in the Vermont collection.

Female.—Length of body 1006μ-1308μ; pre- and postfrontalia, dorsocentralia 1, and postocularia variously fused; typically the pre- and postfrontalia are fused on their respective sides, the dorsocentralia 1 are fused medially, and the postocularia and median eye lie free in the integument; length of fused pre- and postfrontalia 98μ-150μ, width 70μ-84μ; length of fused dorsocentralia 1, 89μ-126μ, width 130μ-178μ. The following variation was found in a few specimens: often the postocularia were fused with the pre- and postfrontalia; occasionally median eye was partially fused with pre- and postfrontalia; occasionally the dorsocentralia 1 were lightly joined to the postfrontalia; and in one case all of these parts were fused to form a frontal shield similar to that shown in Figure 7, except that there was a narrow unsclerotized strip anterior to median eye; dorsolateralia about the same size as fused pre- and postfrontalia; dorsocentralia 2-4 about one-half size of dorsolateralia; dorsocentralia 5 much larger than dorsolateralia; length of genital field 230μ-302μ; genital flaps weakly developed, with a row of setae along median edge; two to four setae on each side anterior to first genital acetabula (Fig. 42); diameter of first genital acetabula 37μ-67μ, second 37μ-62μ, third 42μ-83μ; pregenital sclerite small, located well in front of genital flaps; dorsal lengths of palpal segments: P-I, 51μ-61μ; P-II, 103μ-117μ; P-III, 47μ-58μ; P-IV, 175μ-201μ; P-V, 47μ-53μ; tip of fourth segment usually slightly upcurved. Figure 53 shows chaetotaxy of palp. Dorsal lengths of seg-

ments of second leg: II-Leg-1, 75μ-94μ; II-Leg-2, 108μ-122μ; II-Leg-3, 122μ-150μ; II-Leg-4, 175μ-201μ; II-Leg-5, 220μ-262μ; II-Leg-6, 225μ-272μ; setae at distal end of II-Leg-6 dorsal to claws long and rather sharp-pointed, setae at distal end ventral to claws short and moderately thick. Figure 49 illustrates chaetotaxy of second leg.

The western populations of *P. gorhami* were much more variable than the one eastern population analyzed. Although an application of the "seventy-five percent" rule for separation of subspecies would divide some of these mites up into subspecific groupings, the fact that there is so much intrapopulation variation and the fact that so few populations have as yet been collected and analyzed would seem to make this undesirable, at least at the present time.

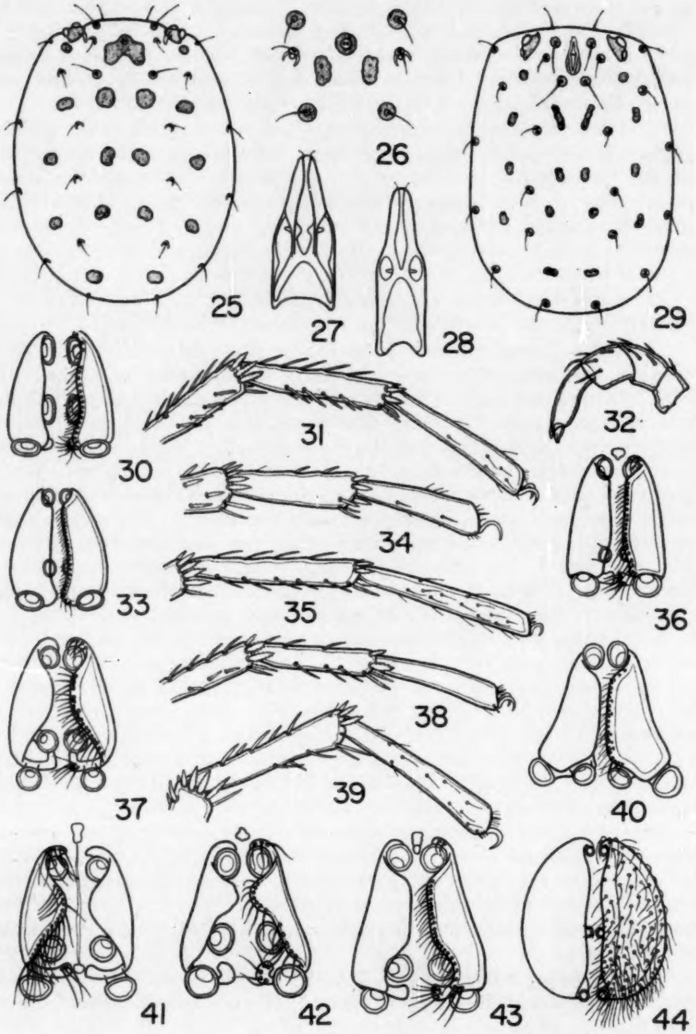
The following range of variation was found in a collection of *P. gorhami* from the South Fork of Iron Creek, Hood County, Oregon.

Female.—Length of body 734μ-1358μ; pre- and postfrontalia, postocularia, and dorsocentralia 1 exhibiting the following variation: (1) with four separate plates (Fig. 4) and the postocularia and median eye free in integument; (2) with two plates, the pre- and postfrontalia enclosing the median eye, and the dorsocentralia 1 fused medially; (3) in one specimen the dorsocentralia 1 were fused medially and joined to the left pre- and postfrontalia, and the postocularia were also joined to the pre- and postfrontalia; (4) most commonly there was a complete frontal plate made up of the fused pre- and postfrontalia, and dorsocentralia 1; the postocularia may or may not be fused with the frontal plate; length of frontal plate 151μ-226μ, width 80μ-199μ; usually with a slight indentation at anterior and posterior ends of frontal plate; pigment in median eye varying from moderately large amount to almost none; length of genital field 183μ-266μ, with two to four setae on each side anterior to first acetabula; diameter of first acetabula 33μ-50μ, second 29μ-47μ, third 37μ-59μ; dorsal lengths of palpal segments: P-I, 41μ-58μ; P-II, 84μ-117μ; P-III, 42μ-56μ; P-IV, 137μ-201μ; P-V, 37μ-52μ; dorsal lengths of segments of second leg: II-Leg-1, 70μ-89μ; II-Leg-2, 84μ-136μ; II-Leg-3, 82μ-145μ; II-Leg-4, 124μ-234μ; II-Leg-5, 147μ-252μ; II-Leg-6, 168μ-250μ.

Male.—Of the seven males taken in this collection, all had a complete frontal shield; length of frontal shield 151μ-176μ, width 101μ-121μ; in most specimens the postocularia were incorporated into the frontal shield; lengths of segments of palp and second leg fell within lower limits of variation of female; genital field without a pregenital sclerite.

The following variation was present in specimens collected in a small stream along the edge of Hungry Horse Dam Reservoir, Flathead County, Montana on July 9, 1954.

Female.—As in the previous population, the plates in the ocular region varied from four separate plates to a complete frontal plate. One specimen exhibited the condition so common in the eastern population, having the right and left prefrontalia fused to their respective postfrontalia, and the dorsocentralia 1 fused medially; length of frontal



Figs. 25-44. — 25. *Thyasides sphagnorum,* dorsal view, male. 26. *Thyasides sphagnorum,* median eye region, female. 27. *Thyas bruzelii,* dorsal view of capitulum, female. 28. *Euthyas truncata,* dorsal view of capitulum, female. 29. *Euthyas truncata,* dorsal view, male. 30. *Thyopsella dictyophora,* genital field, male. 31. *Thyas bruzelii,* end segments of second leg, male. 32. *Thyasides*

plate 191μ-231μ, width 131μ-221μ; dorsal lengths of palpal segments: P-I, 47μ-56μ; P-II, 89μ-108μ; P-III, 39μ-51μ; P-IV, 154μ-192μ; P-V, 44μ-51μ; dorsal lengths of segments of second leg: II-Leg-1, 70μ-89μ; II-Leg-2, 80μ-107μ; II-Leg-3, 96μ-136μ; II-Leg-4, 152μ-210μ; II-Leg-5, 180μ-252μ; II-Leg-6, 196μ-262μ; genital field 234μ-292μ in length; with two or three setae on genital flaps anterior to first genital acetabula; in two specimens, dorsocentralia 3 were completely missing.

Two specimens of *P. gorhami* from a seepage area in Lewis County, Washington fell within the range of variation of the Oregon population.

Range.—Known from New Brunswick, Vermont, Montana, Oregon, and Washington.

Habitat.—This species has been collected in springs, cold streams, and seepage areas. The author has taken *P. gorhami* most commonly in mud and detritus about the roots of aquatic plants.

Remarks.—Only future collecting will show whether the apparent absence of *P. gorhami* from central North America is real or only the result of inadequate sampling. It is interesting that the thyasin which seems to replace *gorhami* in the same habitat in the Midwest is *P.* (*Marshallothyas*) *asopos.*

The structure of the plates in the median eye region, palps, and genital field show that *Thyas ezoensis* described by Imamura (1954) from Japan is really a species of *Panisopsis* very closely related to *P. gorhami.*

PANISOPSIS (PANISOPSIS) PEDUNCULATA (Koenike)

Figs. 9, 41, 61, 43

Thyas pedunculata Koenike 1895. Abhandl. naturw. Ver. Bremen 13:192.
Panisoides or *Panisopsis pedunculata* Mitchell 1953. American Midland Nat. 49:160.
Panisopsis pedunculata Mitchell 1954. Fieldiana, Zool. 35:36.

The following description is based on two mites collected in Johnson Creek, Lake County, Montana on June 30, 1954. Measurements of the holotype of *pedunculata* are intermediate between those of the Johnson Creek specimens.

Female.—Length of body 1208μ; pre- and postfrontalia, dorsocentralia 1 and the postocularia fused into a large frontal plate which is

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sphagnorum, palp, male. 33. *Thyopsella occidentalis*, genital field, male. 34. *Thyas rivalis*, end segments of second leg, female. 35. *Thyas barbigera*, end segments of second leg, male. 36. *Panisus condensatus*, genital field, female. 37. *Panisopsis setipes*, genital field, male. 38. *Thyas stolli*, end segments of second leg, male. 39. *Thyas pachystoma inepta*, end segments of second leg, female. 40. *Thyopsis cancellata*, genital field, male. 41. *Panisopsis pedunculata*, genital field, female. 42. *Panisopsis gorhami*, genital field, female. 43. *Panisus cataphractus*, genital field, female. 44. *Euthyas truncata*, genital field, male.

much wider anteriorly (Fig. 9); length of frontal plate 342μ, width 192μ; median eye with pigment; dorsocentralia and dorsolateralia somewhat variable in size; with the exception of dorsocentralia 1, all dorsocentralia and dorsolateralia are separate; dorsolateralia 1 somewhat teardrop-shaped; length of genital field 392μ; genital flaps moderately well developed, with a row of setae along median edge; five or six setae on each side anterior to first genital acetabula (Fig. 41); Dorsal lengths of palpal segments: P-I, 61μ; P-II, 119μ; P-III, 58μ; P-IV, 173μ; P-V, 42μ; dorsal lengths of segments of second leg: II-Leg-1, 89μ; II-Leg-2, 122μ; II-Leg-3, 103μ; II-Leg-4, 159μ; II-Leg-5, 183μ; II-Leg-6, 197μ; setae at distal end of second leg dorsal to claws somewhat bluntly pointed, setae at distal and ventral to claws short and hair-like or absent. Figure 63 shows chaetotaxy of second leg.

Male.—Similar to female except that it is smaller and has the dorsocentralia 5 fused medially; length of body 955μ; length of frontal shield 312μ, width 185μ; genital field 236μ in length; dorsal lengths of palpal segments: P-I, 47μ; P-II, 100μ; P-III, 49μ; P-IV, 152μ; P-V, 33μ. Figure 61 illustrates chaetotaxy of palp. Dorsal lengths of segments of second leg: II-Leg-1, 77μ; II-Leg-2, 104μ II-Leg-3, 89μ; II-Leg-4, 133μ; II-Leg-5, 151μ; II-Leg-6, 187μ.

The author has two small series of what appear to be a seepage area form of *P. pedunculata*. Both collections, one from Glacier National Park, Montana, and the other from Lewis County, Washington, were from seepage-wetted mosses along the vertical faces of cliffs. The main difference between these mites and *P. pedunculata* from streams seems to be primarily one of size. The following description is based on individuals from both populations.

Female.—Length of body 915μ-1156μ; frontal plate of the individuals from Montana like those of the stream form of *pedunculata;* the frontal plate of the mites from Washington differed slightly in that the posterior end of the plate is proportionally wider and possesses a V-shaped cleft; length of frontal plate 246μ-312μ, width 146μ-166μ; median eye with pigment; dorsocentralia and dorsolateralia variable in size; in some specimens the dorsocentralia 3 were fused medially, in others the dorsocentralia 5 were fused; length of genital field 220μ-272μ; five or six setae on each side anterior to first genital acetabula; dorsal lengths of palpal segments: P-I, 40μ-52μ; P-II, 82μ-108μ; P-III, 42μ-53μ; P-IV, 122μ-161μ; P-V, 33μ-42μ; dorsal lengths of segments of second leg: II-Leg-1, 77μ-89μ; II-Leg-2, 80μ-101μ; II-Leg-3, 75μ-94μ; II-Leg-4, 108μ-136μ; II-Leg-5, 127μ-152μ; II-Leg-6, 152μ-173μ.

Male.—Similar to female except all measurements are slightly smaller.

Range.—*P. pedunculata* is known from Montana, Washington, and British Columbia.

Habitat.—Cold streams and among mosses in seepage areas.

Remarks.—Specimens of the present species may be separated from *gorhami* by the shape of the frontal plate and number of setae anterior to the first acetabula, 2-4 in *gorhami,* 5-6 in *pedunculata.*

Subgenus PANISOIDES Lundblad

Panisoides Lundblad 1926. Ent. Tidskr. 47:208.

Subgenotype.—*Panisoides setipes* (Viets).

Subgeneric diagnosis.—Characteristics of the genus except that the median eye does not contain pigment, and the pre- and postfrontalia, dorsocentralia 1 and the postocularia form a large frontal plate which surrounds the median eye.

PANISOPSIS (PANISOIDES) SETIPES (Viets)

Figs. 8, 37, 50, 55, 64

Thyas setipes Viets 1911. Zool. Anz. 38:332.
Panisoides setipes Lundblad 1926. Ent. Tidskr. 47:208.

Female.—Length of body 1440μ; frontal plate 392μ in length, 323μ in width; posterior half of frontal plate much narrowed (Fig. 64); dorsolateralia 1-4 much larger than dorsocentralia 2-4; dorsocentralia 5 and dorsolateralia 4 extending over onto sides of body; with a median plate at posterior end of body (Fig. 8); length of genital field 279μ; genital flaps well developed, with a row of setae along median edge; five to six setae on genital flaps anterior to first acetabula; dorsal lengths of palpal segments: P-I, 65μ; P-II, 123μ; P-III, 63μ; P-IV, 202μ; P-V, 48μ. Figure 50 shows chaetotaxy of palp. Dorsal lengths of segments of second leg: II-Leg-1, 99μ; II-Leg-2, 148μ; II-Leg-3, 113μ; II-Leg-4, 164μ; II-Leg-5, 180μ; II-Leg-6, 188μ. Figure 55 illustrates chaetotaxy of second leg.

Male.—Length of body 1237μ; frontal plate (Fig. 8) 339μ in length, 317μ in width; dorsocentralia and dorsolateralia similar to those of female; length of genital field 274μ; genital flaps moderately developed, with five or six setae on each side anterior to first acetabula; dorsal lengths of palpal segments: P-I, 56μ; P-II, 111μ; P-III, 55μ; P-IV, 188μ; P-V, 49μ; dorsal lengths of segments of second leg: II-Leg-1, 88μ; II-Leg-2, 120μ; II-Leg-3, 104μ; II-Leg-4, 156μ; II-Leg-5, 166μ; II-Leg-6, 184μ.

Range.—Holarctic; in North America this species is known only from two specimens collected in a spring at the base of Maple River Dam, Emmet County, Michigan (T36N/R4W/S10) in June 1952.

Habitat.—The North American specimens were taken in a cold rheocrene spring.

Remarks.—Both specimens of *P. setipes* were taken at the same time in the same collecting pan. Although numerous other collections were made in the same spot, both before and after finding these two mites, no other specimens were taken. This suggests that *setipes* may occupy a microhabitat which was sampled during this one collection only.

Subgenus MARSHALLOTHYAS Cook

Marshallothyas Cook 1953. Proc. Ent. Soc. Wash. 55:305.

Subgenotype.—Marshallothyas asopos Cook.

Subgeneric diagnosis.—Characters of the genus except that the median eye does not contain pigment, and the pre- and postfrontalia, and dorsocentralia 1 are fused on their respective sides to form elongated plates on either side of the median eye; occasionally these plates fused medially for a short distance posterior to median eye, but never surrounding median eye.

PANISOPSIS (MARSHALLOTHYAS) ASOPOS (Cook)

Marshallothyas asopos Cook 1953. Proc. Ent. Soc. Wash. 55:305.

For a description of this mite, see Cook (1953).

Range.—Known from Michigan and Minnesota.

Habitat.—Springs, cold streams, and seepage areas.

Remarks.—With the presence or absence of pigment in the median eye no longer considered a stable generic character, and in view of the great variation of the plates in the ocular region of *Panisopis s. s.*, it is felt that *Marshallothyas* should be reduced to the rank of subgenus.

Genus PANISUS Koenike

Panisus Koenike 1896. Zool. Anz. 19:356.

Genotype.—Panisus cataphractus (Koenike).

Generic diagnosis.—Pre- and postfrontalia, dorsocentralia 1 and the postocularia fused to form a large frontal plate; median eye without pigment; lateral eyes in capsules; dorsocentralia 5 broadly fused medially; three pairs of genital acetabula; genital flaps with setae located anterior to first acetabula; genital field width not greatly reduced at posterior end; apodemes from lateral eye capsules very long.

PANISUS CATAPHRACTUS (Koenike)

Figs. 2, 3, 43, 47, 58

Thyas cataphracta Koenike 1895. Abhandl. naturw. Ver. Bremen 13:196.
Panisus cataphracta Mitchell 1953. Amer Midland Nat. 49:160.
P. cataphracta Mitchell 1954. Fieldiana, Zool. 35:36.
Panisus cataphractus Habeeb 1954. Leaflets Acadian Biol. no. 2:2.

Female.—Length of body 910μ-1920μ; pre- and postfrontalia, dorsocentralia 1 and postocularia fused into a frontal plate wider than long, length of frontal plate 331μ-460μ, width 366μ-702μ; degree of secondary sclerotization around margin of frontal plate (as in dorsocentralia and dorsolateralia) extremely variable; see Figs. 2 and 3 for contrast that may be found, even within a single population; dorsocentralia 5 fused medially, sometimes enclosing dorsoglandularia 7 (Fig. 2); genital flaps well developed, length of genital field 279μ-340μ, with two setae on each side anterior to first acetabula (Fig. 43); dorsal lengths of palpal segments: P-I, 48μ-60μ; P-II, 96μ-121μ; P-III, 56μ-65μ; P-IV, 156μ-180μ; P-V, 38μ-53μ; chaetotaxy of palp variable. Figure 47 illustrates more typical type; dorsal lengths of

segments of second leg: II-Leg-1, 88μ-104μ; II-Leg-2, 116μ-146μ; II-Leg-3, 124μ-148μ; II-Leg-4, 199μ-244μ; II-Leg-5, 198μ-249μ; II-Leg-6, 226μ-262μ. Figure 58 shows chaetotaxy of second leg.

Male.—Similar to female except smaller; length of body 1170μ-1281μ; length of frontal plate 302μ-331μ, width 401μ-489μ; length of genital field 209μ-244μ; dorsal lengths of palpal segments: P-I, 44μ-47μ; P-II, 88μ-102μ; P-III, 44μ-56μ; P-IV, 132μ-148μ; P-V, 41μ-44μ; dorsal lengths of segments of second leg: II-Leg-1, 78μ-84μ; II-Leg-2, 104μ-116μ; II-Leg-3, 96μ-112μ; II-Leg-4, 160μ-181μ; II-Leg-5, 176μ-188μ; II-Leg-6, 192μ-214μ.

Range.—The type locality was designated as the Kit-a-mun River. Although this area cannot be located with certainty, the evidence seems to indicate that it is a branch of the Kootenay River in southeastern British Columbia. This species has also been collected in Montana, Minnesota, Michigan, Ontario, and New Brunswick.

Habitat.—Springs, cold streams, and seepage areas.

Remarks.—*P. cataphractus* differs from the following species, *P. condensatus,* in being larger, having proportionally longer and narrower legs, and having secondary sclerotization often present as small irregular lobes along edges of dorsal plates.

PANISUS CONDENSATUS Habeeb

Figs. 6, 36, 59, 66

Panisus condensatus Habeeb 1954. Leaflets Acadian Biol. no. 2:1.
P. condensatus Habeeb 1954. *Ibid.* no. 4:8.

Female.—(measurements based on two individuals) Length of body 990μ-1215μ; pre- and postfrontalia, dorsocentralia 1 and postocularia fused into a frontal plate 222μ-297μ in length, 349μ-437μ in width (Fig. 6); length of genital field 203μ-253μ; with two setae on each side anterior to first acetabula (Fig. 36); secondary sclerotization producing only a small amount of lobing along edges of dorsal sclerites; dorsal lengths of palpal segments: P-I, 42μ-56μ; P-II, 73μ-96μ; P-III, 38μ-49μ; P-IV, 116μ-141μ; P-V, 32μ-43μ. Figure 59 shows chaetotaxy of palp. Dorsal lengths of segments of second leg: II-Leg-1, 60μ-82μ; II-Leg-2, 88μ-116μ; II-Leg-3, 73μ-104μ; II-Leg-4, 117μ-162μ; II-Leg-5, 128μ-168μ; II-Leg-6, 152μ-192μ. Figure 66 illustrates chaetotaxy of second leg.

Male.—Similar to female except that it averages somewhat smaller.

Range.—Known from Indiana, Minnesota, New Jersey, and New Brunswick.

Habitat.—Streams.

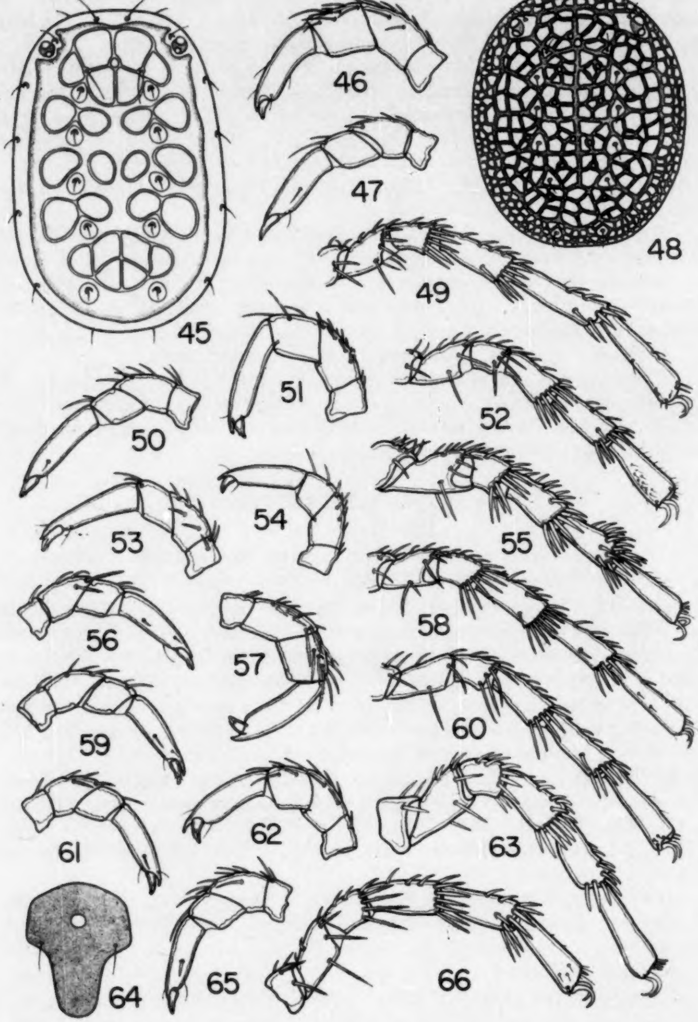
Remarks.—See remarks under *Panisus cataphractus.*

Genus THYOPSELLA Cook

Thyopsella Cook 1955. Amer. Midland Nat. 53:412.

Genotype.—*Thyopsella dictyophora* Cook.

Generic diagnosis.—Dorsal plates incorporated into a dorsal shield



Figs. 45-66. — 45. *Thyopsella occidentalis,* dorsal view, male. 46. *Euthyas truncata,* palp, male. 47. *Panisus cataphractus,* palp, female. 48. *Thyopsis cancellata,* dorsal view, male. 49. *Panisopsis gorhami,* second leg, female. 50. *Panisopsis setipes,* palp, male. 51. *Thyas bruzelii,* palp, male. 52. *Thyopsella occidentalis,* second leg, male. 53. *Panisopsis gorhami,* palp, female. 54. *Thyas*

in the adult stage; lateral eyes in capsules; median eye without pigment; frontal plate made up of fused pre- and postfrontalia, postocularia, dorsocentralia 1 and dorsolateralia 1; dorsocentralia 2 and 4 fused medially with their respective dorsolateralia; dorsocentralia 5 fused medially; dorsoglandularia 3-7 lying in clear areas in the integument; three pairs of genital acetabula, posterior pair somewhat elliptical.

THYOPSELLA DICTYOPHORA Cook

Figs. 30, 60

Thyopsella dictyophora Cook 1955. Amer. Midland Nat. 53:412.

For a description of this mite, see Cook (1955).

Range.—The type locality of this species is a spring in Emmet County, Michigan. *T. dictyophora* has since been collected in a seepage area associated with Laughing Whitefish Falls in the Upper Peninsula of Michigan (Mitchell Coll.) and in a rheocrene spring in Boulder County, Colorado.

Habitat.—Cold springs and seepage areas.

Remarks.—See remarks under *Thyopsella occidentalis.*

Thyopsella occidentalis, new species

Figs. 33, 45, 52, 56

Male.—Length of dorsal shield 786μ-1035μ, width of dorsal shield 541μ-629μ; dorsal shield elliptical, truncate at anterior end; lateral eyes in capsules, not incorporated into dorsal shield (Fig. 45); dorsal shield not reticulate; frontal plate made up of fused pre- and postfrontalia, dorsocentralia 1 and dorsolateralia 1; dorsocentralia 2 and 4 fused with their respective dorsolateralia; dorsocentralia 3 slightly separated from dorsolateralia 3; dorsoglandularia 3-7 lying in clear areas on dorsal shield; lateroglandularia lying laterad to dorsal shield; length of genital field 196μ-208μ; third pair of genital acetabula elliptical, first and second pairs more nearly round (Fig. 33); dorsal lengths of palpal segments: P-I, 41μ-45μ; P-II, 84μ-92μ; P-III, 44μ-48μ; P-IV, 128μ-144μ; P-V, 36μ-40μ. Figure 56 shows chaetotaxy of palp. Dorsal lengths of segments of second leg: II-Leg-1, 64μ-72μ; II-Leg-2, 96μ-108μ; II-Leg-3, 80μ-88μ; II-Leg-4, 118μ-128μ; II-Leg-5, 132μ-144μ; II-Leg-6, 160μ-172μ. Figure 52 illustrates chaetotaxy of second leg.

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stolli, palp, male. 55. *Panisopsis setipes,* second leg, male. 56. *Thyopsella occidentalis,* palp, male. 57. *Thyas barbigera,* palp, female. 58. *Panisus cataphractus,* second leg, female. 59. *Panisus condensatus,* palp, female. 60. *Thyopsella dictyophora,* second leg, male. 61. *Panisopsis pedunculata,* palp, female. 62. *Thyas rivalis,* palp, female. 63. *Panisopsis pedunculata,* second leg, female. 64. *Panisopsis setipes,* frontal plate, female. 65. *Thyopsis cancellata,* palp, female. 66. *Panisus condensatus,* second leg, female.

Female.—Similar to male except that it averages slightly larger; length of dorsal shield 1170μ-1282μ, width 680μ-786μ; segment lengths of both palp and second leg slightly larger than male; small pregenital sclerite present.

Types.—Holotype, adult male, collected in the Madison River, Yellowstone National Park, Wyoming, on July 5, 1954; allotype, adult female, same data; paratypes, 4 males, 5 females, 2 nymphs, same data. The holotype and allotype will be placed in the Chicago Natural History Museum, paratypes in the United States National Museum.

Habitat.—In contrast to *T. dictyophora,* the present species seems to be an inhabitant of larger and warmer streams.

Remarks.—*Thyopsella occidentalis* may be differentiated from *T. dictyophora* as follows: The lateral eyes and dorsoglandularia 2 are not included in the dorsal shield of *occidentalis.* The dorsal shield of the new species, in contrast to *dictyophora,* is not reticulate, and the legs of *occidentalis* are much stockier (compare Figs. 52 and 60).

Genus THYOPSIS Piegsig

Thyopsis Piersig 1899. Zoologica 19(22):409.

Genotype.—*Thyopsis cancellata* (Protz).

Generic diagnosis.—Dorsal plates incorporated into a reticulate dorsal shield in both adult and nymph; lateral eyes in capsules; median eye without pigment; dorsal plates occupying most of the area of the dorsal shield; three pairs of genital acetabula, second pair near posterior end of genital field; chelicera not long and stylet-like.

THYOPSIS CANCELLATA (Protz)

Figs. 40, 48, 65

Thyas cancellata Protz 1896. Zool. Anz. 19:408.

Female.—(the following measurements are based on four specimens) Length of dorsal shield 1192-1455μ, width 945μ-1095μ; dorsal shield elliptical; lateral eyes in capsules, these incorporated into the dorsal shield; dorsal shield reticulate (Fig. 48), degree of reticulation variable; pre- and postfrontalia, dorsocentralia, and dorsolateralia occupying most of dorsal surface; reticulations extending beyond dorsal plates; dorsoglandularia 2-7 lying on dorsal shield; lateroglandularia lying laterad to dorsal shield; length of genital field 267μ-326μ; genital acetabula more or less round; second pair of acetabula lying medial to third pair (Fig. 40); dorsal lengths of palpal segments: P-I, 39μ-52μ; P-II, 110μ-122μ; P-III, 52μ-60μ; P-IV, 139μ-168μ; P-V, 40μ-43μ; Figure 65 illustrates chaetotaxy of palp; dorsal lengths of segments of second leg: II-Leg-1, 80μ-104μ; II-Leg-2, 112μ-128μ; II-Leg-3, 76μ-104μ; II-Leg-4, 108μ-136μ; II-Leg-5, 128μ-146μ; II-Leg-6, 124μ-152μ.

Male.—No specimens taken.

Range.—Holarctic; in North America, *T. cancellata* has been collected in Michigan and Ontario (Mitchell Coll.).

Habitat.—This species has an extremely wide habitat tolerance. In North America it has been taken in temporary ponds and seepage areas. In Europe, *cancellata* is also known from springs and even brackish water. Although it is found in a wide variety of habitats, the presence of short, powerful legs with numerous, thickened setae suggests that it evolved in a seepage habitat and has secondarily invaded others.

Genus TRICHOTHYAS Viets

Trichothyas Viets 1926. Zool. Anz. 69:191.

Genotype.—*Trichothyas pennata* (Viets).

Generic diagnosis.—Pre- and postfrontalia, postocularia, dorsocentralia 1 and 2 fused to form a large frontal plate; median eye without pigment; lateral eyes in capsules; dorsocentralia 3 and 4 fused medially; six or more genital acetabula; genital flaps much reduced, especially in male; distal end of third segment of first leg without a spine-like projection in males.

Subgenus LUNDBLADIA Viets

Lundbladia Viets 1929. Zool. Anz. 86:49.

Subgenotype.—*Lundbladia feuerborni* Viets.

Subgeneric diagnosis.—Characters of the genus; three pairs of genital acetabula; posterior acetabula touching genital flaps in males; genital flaps extending well beyond anterior edge of third acetabula in females.

TRICHOTHYAS (LUNDBLADIA) MUSICOLA (Mitchell)

Lundbladia musicola Mitchell 1953. Amer. Midland Nat 49:162.
L. musicola Mitchell 1954. Fieldiana, Zool. 35:36.

For a description of this species, see Mitchell (1953).

Range.—At the present time *T. musicola* is known only from the type locality, a seepage area in Rock Creek Canyon, Kankakee County, Illinois.

KEY TO THE GENERA, SUBGENERA, AND SPECIES OF THYASINAE KNOWN TO OCCUR IN NORTH AMERICA

1. Dorsum covered by a large dorsal shield (Figs. 45, 48) 2

2. Second pair of genital acetabula located near posterior end of the genital flaps (Fig. 40) .... Genus *Thyopsis* Piersig
(only known North American species, *T. cancellata* Protz)

2. Second pair of genital acetabula located almost midway between the anterior and posterior ends of the genital flaps (Figs. 30, 33) .... Genus *Thyopsella* Cook 3

3. Lateral eyes and dorsoglandularia 2 incorporated into the dorsal shield; dorsal shield reticulate .... *T. dictyophora* Cook

3. Lateral eyes and dorsoglandularia 2 not incorporated into the dorsal shield; dorsal shield not reticulate (Fig. 45) .... *T. occidentalis* new species

1. Dorsum not covered by a large dorsal shield, although the greatly expanded sclerites may occupy most of the dorsal surface (Fig. 2) 4

4. Pre- and postfrontalia, dorsocentralia 1 and 2 united into a frontal plates; dorsocentralia 3 and 4 fused medially .... Genus *Trichothyas* Viets (only described North American species, *T.* (*Lundbladia*) *musicola* (Mitchell)

4. Degree of fusion of the pre- and postfrontalia, dorsocentralia 1 various; frontal plate, if present, not including the dorsocentralia 2; dorsocentralia 3 and 4 almost never fused medially 5

5. Pre- and postfrontalia fused into a small, spindle-shaped frontal plate (Fig. 29); median eye pigmented .... Genus *Euthyas* Piersig (only described species, *E. truncata* (Neuman)

5. Pre- and postfrontalia either not fused or, if fused, not forming a small, spindle-shaped frontal plate 6

6. Genital flaps extending beyond the first genital acetabula; two or more stout setae present anterior to the first acetabula (Figs. 41-43) 7

7. Genital flaps broad at posterior end (Figs. 36, 43); dorsocentralia 5 fused medially; apodemes of eye capsules very long (Figs. 2, 3, 6) .... Genus *Panisus* Koenike

8. Legs relatively long and thin; last segment of second leg four times as long as wide (Fig. 58) .... *P. cataphractus* (Koenike)

8. Legs relatively short and stocky; last segment of second leg slightly over three times as long as wide (Fig. 66) .... *P. condensatus* Habeeb

7. Genital flaps narrowed at posterior end (Figs. 37, 41, 42); dorsocentralia 5 usually not fused medially; apodemes of eye capsules short (Figs. 7-9) .... Genus *Panisopsis Viets* 9

9. Median eye never pigmented 10

10. Median eye completely surrounded by a plate made up of the fused pre- and postfrontalia, and dorsocentralia 1 (Fig. 8) .... Subgenus *Panisoides* Lundblad (only described species, *P.* (*Panisoides*) *setipes* (Viets)

10. Median eye flanked on either side by two separate plates made up of the fused pre- and postfrontalia, and dorsocentralia 1 .... Subgenus *Marshallothyas* Cook (only described species, *P. (Marshallothyas) asopos* (Cook)

9. Median eye usually with pigment, although amount of pigment sometimes much reduced .... Subgenus *Panisopsis* Viets 11

11. With 2-4 setae on each genital flap anterior to the first genital acetabulum (Fig. 42); frontal plates varying from four separate plates to a completely fused single plate (Figs. 4, 5, 7) .... *P. (Panisopsis) gorhami* (Habeeb)

11. With 5-6 setae on each genital flap anterior to the first genital acetabulum (Fig. 41); with a single frontal plate (Fig. 9) .... *P. (Panisopsis) pedunculata* (Koenike)

6. Genital flaps not extending beyond the first genital acetabula; setae absent anterior to the first acetabula (Figs. 13-15)................12

12. Median eye usually surrounded by a plate made up of the fused pre- and postfrontalia (Fig. 25), occasionally with separate plates (Fig. 26); second and third genital acetabula very close together (Figs. 20, 21).....................Genus *Thyasides* Lundblad (only described North American species, *T. sphagnorum* Habeeb)

12. Median eye lying free in the integument (Fig. 10); second and third genital acetabula separated by a moderate distance (Figs. 11, 13, 17, 18)..........................Genus *Thyas* Koch........13

13. Median eye with pigment............Subgenus *Zschokkea* Koenike (only known North American species, *T. (Zschokkea) bruzelii* Lundblad)

13. Median eye without pigment..........Subgenus *Thyas* Koch........14

14. Second and third genital acetabula on a common sclerotized base (Figs. 13, 14, 17; the second genital acetabula lying more or less medial or anteriomedial to the third acetabula...15

15. Second pair of genital acetabula located anteriomedial to the third pair (Fig. 17); distal segments of second leg relatively long and narrow (Fig. 35)...................... ....*T. (Thyas) barbigera* Viets

15. Second pair of genital acetabula located medial to the third pair (Figs. 13, 14); distal segments of the second leg relatively short (Fig. 38)............................ ....*T. (Thyas) stolli* Koenike)

14. Second and third genital acetabula not lying on a common sclerotized base (Figs. 15, 18); the second genital acetabula lying more or less anterior to the third acetabula 16

16. Pre- and postfrontalia fused into plates similar in size and shape to the dorsocentralia (Fig. 12); end segments of the second leg relatively short and stocky (Fig. 34) ....*T. (Thyas) rivalis* Koenike

16. Pre- and postfrontalia separate or, if fused, they are much smaller than the dorsocentralia (Fig. 10); end segments of the second leg relatively long and narrow (Fig. 39)............*T. (Thyas) pachystoma inepta* Lundblad

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Hormonal Regulation of the Distal Retinal Pigment of Crayfishes, and the Effects of Long Exposure to Light and Darkness[1]

MILTON FINGERMAN, WILLIAM C. MOBBERLY, JR., AND BANGALORE I. SUNDARARAJ
Newcomb College, Tulane University, New Orleans

The distal retinal pigment of crustaceans will move toward the fully light-adapted position after injection of extracts of eyestalks. This observation, first reported by Kleinholz (1936) for the prawn, *Palaemonetes vulgaris,* has since been repeated with several other crustaceans. Welsh (1939), the first investigator to study endocrine control of retinal pigments in crayfishes, found a retinal pigment light-adapting hormone in the eyestalks of *Cambarus bartoni.* More recently, Brown, Hines, and Fingerman (1952) provided the first evidence that a distal retinal pigment light-adapting hormone exists in the supraesophageal ganglia of *Palaemonetes vulgaris.* This hormone has also been found in the eyestalks and supraesophageal ganglia of the crayfishes *Cambarellus shufeldti* and *Orconectes clypeatus* (Fingerman, 1956, 1957a; Fingerman, Lowe, and Sundararaj, 1959a).

Indirect evidence for a distal retinal pigment dark-adapting hormone in *Palaemonetes* was presented by Brown, Hines, and Fingerman (1952). Their evidence was based on differences in rates of dark-adaptation between control prawns and those injected with extracts of various organs. Fingerman later (1957a) postulated the existence of a distal retinal pigment dark-adapting hormone in the dwarf crayfish, *Cambarellus shufeldti.* Crayfish that had been put in darkness for 20 minutes continued to dark-adapt for approximately 15 minutes after their return to light. Presumably a dark-adapting hormone was released into the circulation when the specimens were placed in darkness and continued to act after the crayfish were returned to light.

Fingerman, Lowe, and Sundararaj (1959a) supplied the first direct evidence for a distal retinal pigment dark-adapting hormone in a crayfish, *Orconectes clypeatus.* These investigators were able to separate (by filter paper electrophoresis at pH 7.2) the light-adapting and dark-adapting hormones in extracts of supraesophageal ganglia with the circumesophageal connectives attached. The light-adapting hormone was electropositive; the dark-adapting hormone was electronegative. Assay specimens were kept in black containers under an illumination of such intensity that the distal pigment was in a position approximately midway between the full light-adapted and dark-adapted states.

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Fingerman, Lowe, and Sundararaj (1959b) found a dark-adapting hormone in specimens of *Palaemonetes vulgaris* by a different procedure. Illuminated specimens whose distal retinal pigments were in a position approximately midway between the fully light-adapted and dark-adapted positions were injected with extracts of eyestalks. The initial response was a light-adaptational one that lasted two hours. A dark-adaptational response followed and lasted approximately five hours. The dark-adapting hormone had remained in the blood during the two hours the light-adapting hormone was active.

In the present study the investigators wished to learn, first of all, if the delayed response observed with the distal retinal pigment dark-adapting hormone of *Palaemonetes* would occur if the same procedure were used with other crustaceans. The organisms chosen were the crayfishes *Orconectes clypeatus* and *Cambarellus shufeldti.* Use of organisms in a suborder different from that of *Palaemonetes* would yield some insight into the extent of the delayed response among crustaceans. The second aim of this investigation was to determine the effects in *Cambarellus* of long-term adaptation under illumination, and in darkness, upon the amount of light-adapting hormone in the supraesophageal ganglia.

MATERIALS AND METHODS

Individuals of the crayfishes *Orconectes clypeatus* and *Cambarellus shufeldti* were collected at Hickory, Louisiana, for use in the experiments described below. The crayfishes were constantly illuminated in the laboratory. They were kept in aquaria that contained dechlorinated tap water approximately 2.5 cm deep.

The method of Sandeen and Brown (1952), as modified by Fingerman (1957a) for use with crayfishes, was employed to facilitate rapid determination of the state of the distal retinal pigment. All extracts in the experiments described below were assayed on specimens of *Cambarellus.* The specimens were placed one at a time, ventral surface down, on the stage of a stereoscopic dissecting microscope. With the aid of an ocular micrometer and transmitted light the following measurements were made: (1) the width of the translucent distal portion of the compound eye in a plane parallel to the long axis of the eyestalk and (2) the length of the eye from the corneal surface to the apex of the notch at the proximal portion of the eye. The ratio of length of clear area (measurement 1) to total length (measurement 2) is known as the distal pigment index. Use of this ratio minimizes effects of size differences.

To render the distal clear portion of the eye more transparent and the proximal edge of the clear area more definite, the *Cambarellus* were submerged in a dish of water on the stage of the microscope. A magnification of 60X was used in the measurements. Each unit of the ocular micrometer was equivalent to 24.4 μ.

In the fully dark-adapted eye the distal retinal pigment abutted

against the cornea; the distal pigment index was 0.00. In the fully light-adapted eye of *Cambarellus* the distal pigment index was about 0.12. The distal pigment index of 10 crayfish could be determined with ease in three minutes. For all experiments the assay animals were kept in black enameled pans containing aerated tap water approximately 2.5 cm deep. Ten animals were in each pan. These pans were kept under an illumination of 30 ft-c. At this intensity the distal retinal pigment was approximately midway between the fully light-adapted and dark-adapted states. In all but one group of experiments the assay animals were exposed to constant illumination in the laboratory for two weeks. The 24-hour rhythm of migration of the distal retinal pigment of *Cambarellus* is no longer apparent in specimens kept under constant illumination for 14 days (Fingerman, and Lowe, 1957a).

One eyestalk had been removed from each of the assay animals, *Cambarellus,* at least 12 hours before use in an experiment. Removal of one eyestalk results in loss of an important source of retinal pigment light-adapting hormone (Fingerman, 1957a). Presumably, therefore, antagonism of a dark-adapting substance that might be injected would not occur as readily as in intact specimens.

The tissue extracts were prepared as follows. The desired number of organs for an experiment was dissected out and placed with a minimum of saline in a glass mortar. The organs were triturated and then suspended in a sufficient volume of Van Harreveld's solution (Van Harreveld, 1936) to yield a concentration of one-third of a complement per 0.02 ml of extract. Every extract was assayed on 10 animals.

The results of the statistical treatment of the data obtained in all experiments are presented in Table I. Student's t test was used for determination of the level of significance. The 5% level was taken as the maximum for a significant difference between the two means.

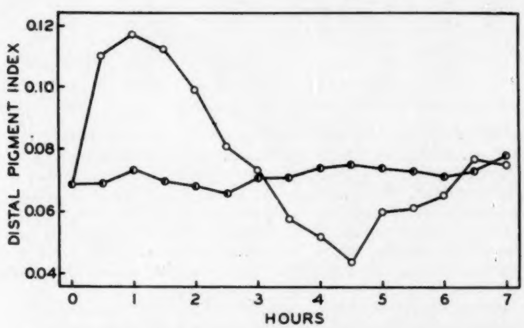

Fig. 1.—Responses of the distal retinal pigment of *Cambarellus* to extracts of eyestalks (circles). Half-filled circles, control.

EXPERIMENTS AND RESULTS

RESPONSES IN CAMBARELLUS TO EXTRACTS OF SINUS GLANDS AND CENTRAL NERVOUS ORGANS OF CAMBARELLUS

The object of this series of experiments was to determine if direct evidence could be adduced for a distal retinal pigment dark-adapting hormone in the sinus gland and central nervous organs of *Cambarellus*

TABLE I.—Results of assays for distal retinal pigment light-adapting and dark-adapting hormones in tissues of *Cambarellus* and *Orconectes*. N, number of pigment indices used in the calculations; S.D., standard deviation; S.E., standard error of the difference between the means of the experimental (E) and control (C) animals; t, Student's t.

Experiments*		N	Range	Mean	S.D.	S.E.	t
1.	E	56	0.07-0.14	0.113	0.018	0.0033	13.0
	C	53	0.04-0.10	0.072	0.016		
2.	E	27	0.00-0.08	0.044	0.029	0.0058	2.77
	C	25	0.05-0.09	0.075	0.009		
3.	E	149	0.04-0.18	0.096	0.026	0.0027	6.29
	C	140	0.00-0.13	0.079	0.020		
4.	E	149	0.05-0.18	0.115	0.025	0.0027	4.17
	C	146	0.00-0.13	0.078	0.020		
5.	E	38	0.00-0.09	0.049	0.024	0.0047	4.22
	C	39	0.04-0.10	0.071	0.016		
6.	E	60	0.08-0.18	0.116	0.020	0.0036	12.22
	C	60	0.04-0.10	0.073	0.015		
7.	E	38	0.00-0.10	0.062	0.024	0.0048	2.38
	C	37	0.02-0.10	0.073	0.017		
8.	E	30	0.07-0.13	0.098	0.014	0.0039	6.21
	C	30	0.04-0.10	0.073	0.016		
9.	E	30	0.10-0.15	0.126	0.016	0.0041	13.7
	C	30	0.05-0.10	0.075	0.015		
10.	E	29	0.00-0.10	0.057	0.021	0.0053	3.87
	C	29	0.04-0.11	0.076	0.019		
11.	E	29	0.08-0.14	0.109	0.019	0.0042	8.35
	C	30	0.05-0.10	0.075	0.015		
12.	E	28	0.04-0.10	0.063	0.016	0.0046	3.22
	C	29	0.04-0.11	0.078	0.018		
13.	L	80	0.04-0.15	0.096	0.022	0.0036	4.27
	D	79	0.06-0.18	0.117	0.024		

Exp.* 1.—Light-adapting hormone in eyestalk of *Cambarellus*.
Exp. 2.—Dark-adapting hormone in eyestalk of *Cambarellus*.
Exp. 3.—Light-adapting hormone in sinus gland of *Cambarellus*.
Exp. 4.—Light-adapting hormone in optic ganglia of *Cambarellus*.
Exp. 5.—Dark-adapting hormone in optic ganglia of *Cambarellus*.
Exp. 6.—Light-adapting hormone in supraesophageal ganglia of *Cambarellus*.
Exp. 7.—Dark-adapting hormone in supraesophageal ganglia of *Cambarellus*.
Exp. 8.—Light-adapting hormone in circumesophageal connectives of *Cambarellus*.
Exp. 9.—Light-adapting hormone in optic ganglia of *Orconectes*.
Exp. 10.—Dark-adapting hormone in optic ganglia of *Orconectes*.
Exp. 11.—Light-adapting hormone in supraesophageal ganglia of *Orconectes*.
Exp. 12.—Dark-adapting hormone in supraesophageal ganglia of *Orconectes*.
Exp. 13.—Light-adapting hormone in supraesophageal ganglia of *Cambarellus* kept for 17 days in light (L) and in darkness (D).

with the method of Fingerman, Lowe, and Sundararaj (1959b) that was described above.

In each of the first three experiments 10 crayfish received extracts of eyestalks and 10 received Van Harreveld's solution as a control. The data of the three experiments were consistent and were averaged. The means are shown in Figure 1. A light-adaptational response was apparent. It lasted three hours and was followed by a dark-adaptational response that lasted an additional 3.5 hours. Both effects were statistically significant when compared with the controls, the light-adaptational response at the 0.1% level (Table I, Exp. 1) and the dark-adaptational one at the 1.0% level (Table I, Exp. 2). Calculations of the statistical significance of the light-adaptational response as compared with the control animals were based on the distal pigment indices determined 60 and 90 minutes after injection of the extracts. The readings made at 4.5 hours were used to calculate the significance of the dark-adaptational response.

The next experiment involved analysis of the results of injection of the components of the eyestalk, the sinus gland and optic ganglia, to determine if both structures possess the two retinal pigment hormones. This is the only experiment in which recently collected assay animals were used. They still showed signs of the 24-hour rhythm of pigment migration wherein the pigment is maximally light-adapted near noon, exemplified by the control curve in Figure 2; the peak occurred at approximately 11 AM, two hours after the beginning of the experiment. The experiment was performed five timcs. The data were averaged and presented in Figure 2.

The curve depicting the responses of *Cambarellus* to extracts of

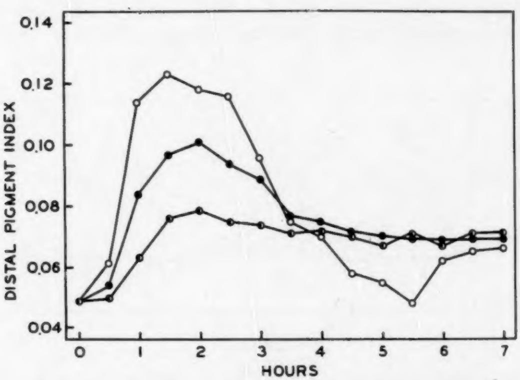

Fig. 2.—Responses of the distal retinal pigment of *Cambarellus* to extracts of optic ganglia (circles) and sinus glands (dots). Half-filled circles, control.

optic ganglia is similar to that shown in Figure 1 for the entire eyestalk, *i.e.*, both retinal pigment hormones are found in the optic ganglia. The calculated values of the significance level of the differences between the control group and the specimens that received extracts of the optic ganglia are 0.1% for light-adaptation and 5.0% for dark-adaptation (Table I, Exp. 4 and 5).

On the other hand, the sinus gland had less light-adapting hormone than the optic ganglia and no dark-adapting hormone. The difference between the degree of light-adaptation produced by the extracts of the two tissues was significant at the 0.1% level. Calculations in this case were based on the readings made after 90, 120, and 150 minutes. The degree of light-adaptation produced by the sinus gland extracts was statistically significant at the 0.1% level based on calculations employing the readings made after 90, 120, and 150 minutes (Table I, Exp. 3). The absence of a dark-adapting effect when extracts of the sinus gland were used proved that the dark-adapting responses were not caused by over-compensation on the part of the organism in removing injected light-adapting hormone from the blood but must have been caused by a dark-adapting substance.

The final experiment of this series involved the assay of the supraesophageal ganglia and circumesophageal connectives of freshly collected *Cambarellus* for light- and dark-adapting hormones. This procedure was employed four times. The results were averaged and presented in Figure 3. The supraesophageal ganglia contained more light-adapting hormone than the circumesophageal connectives. This difference was significant at the 0.1% level. The calculations were based on the readings made after 60 and 90 minutes. The supraesophageal ganglia contained a statistically significant quantity (5.0% level) of dark-adapting hormone (Table I, Exp. 7), the circumesophageal connectives did not. The calculations for dark-adapting hormone were based on the readings made after five hours. The

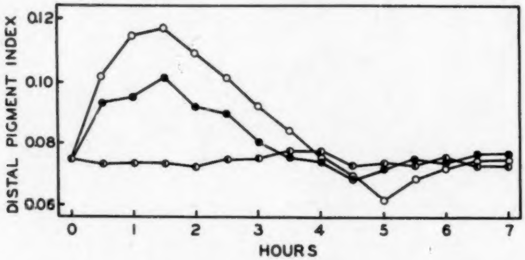

Fig. 3.—Responses of the distal retinal pigment of *Cambarellus* to extracts of supraesophageal ganglia (circles) and circumesophageal connectives (dots). Half-filled circles, control.

amounts of light-adapting hormone in the supraesophageal ganglia and in the circumesophageal connectives, as compared with the controls, were significant at the 0.1% level (Table I, Exp. 6 and 8). The calculations were based on the readings made after 60 and 90 minutes for the supraesophageal ganglia and the readings made after 90 minutes for the circumesophageal connectives.

RESPONSES IN CAMBARELLUS TO EXTRACTS OF TISSUES OF ORCONECTES

The object of this group of experiments was to determine the response of one-eyed *Cambarellus* to extracts of tissues of *Orconectes* to learn if the sources of retinal pigment hormones in the latter crayfish are similar to those in *Cambarellus*.

Extracts of the optic ganglia and supraesophageal ganglia were assayed three times. Both structures contained retinal pigment light-adapting and dark-adapting hormones. The averaged data are presented in Figure 4. The data were analyzed statistically. The degrees of light- and dark-adaptation induced by the optic ganglia were significant at the 0.1% level (Table I, Exp. 9 and 10). The calculations were based on the readings made after 90 minutes for light-adaptation and the readings made after 4.5 hours for dark-adaptation. The effects of the supraesophageal ganglia were significant at the 0.1% and 1.0% levels for the light- and dark-adapting hormones respectively (Table I, Exp. 11 and 12). The calculations were based on the readings made after 90 minutes for light-adaptation and on the four hour readings for dark-adaptation.

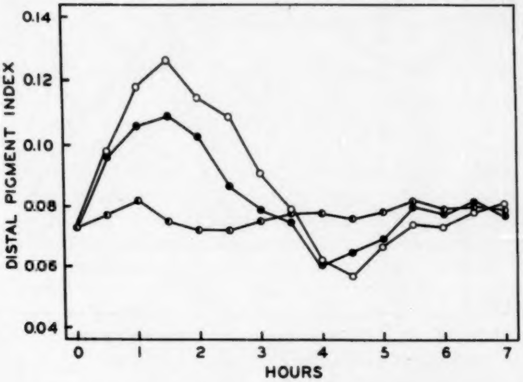

Fig. 4.—Responses of the distal retinal pigment of *Cambarellus* to extracts of optic ganglia (circles) and supraesophageal ganglia (dots) of *Orconectes*. Half-filled circles, control.

INFLUENCE OF LIGHT AND DARKNESS UPON THE AMOUNT OF LIGHT-ADAPTING HORMONE IN THE SUPRAESOPHAGEAL GANGLIA OF CAMBARELLUS

The aim of this series of experiments was to determine if maintenance of *Cambarellus* in darkness and under illumination would induce a change in the amount of light-adapting hormone in the supraesophageal ganglia.

Specimens were collected and brought to the laboratory where they were immediately divided into two groups. One lot was placed in darkness and the second group was placed on a white background under an illumination of 135 ft-c. The crayfish were kept in these locations for 17 days when the supraesophageal ganglia of the two groups were assayed for light-adapting hormone.

The same procedure was performed four times. The results were the same each time. Therefore, the data for the four experiments were averaged. The results are presented in Figure 5.

As is apparent from inspection of the figure, the supraesophageal ganglia of the individuals left in darkness contained more light-adapting hormone than the supraesophageal ganglia of dwarf crayfish kept under constant illumination. Statistical analysis revealed that

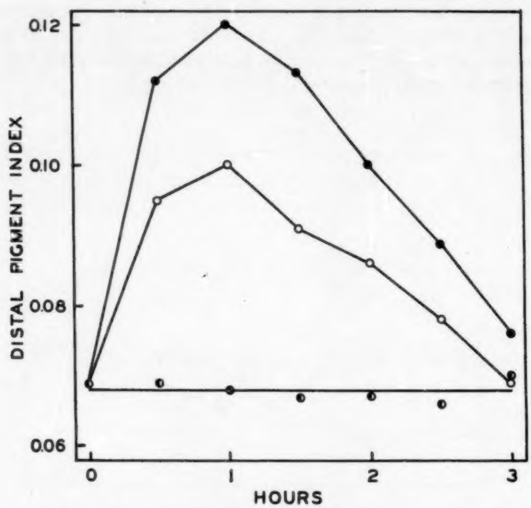

Fig. 5.—Responses of the distal retinal pigment of *Cambarellus* to extracts of supraesophageal ganglia of *Cambarellus* maintained for 17 days on a white background under illumination of 135 ft.-c. (circles) and in darkness (dots). Half-filled circles, control.

the curves depicting the average responses to extracts of the supraesophageal ganglia from the two groups were different from each other at the 0.1% level of significance (Table I, Exp. 13). The readings made after 60 and 90 minutes were used in the calculations.

DISCUSSION

The results of these experiments help to elucidate the mechanism controlling migration of the distal retinal pigment in *Cambarellus*. The results obtained with extracts of tissues from the crayfishes *Orconectes clypeatus* and *Cambarellus shufeldti* were qualitatively similar to the results of Fingerman, Lowe, and Sundararaj (1959b) obtained with *Palaemonetes vulgaris*. In dwarf crayfish the light-adapting effect lasted approximately 3-3.5 hours with the concentrations of materials used herein. The subsequent dark-adaptational response lasted approximately 2-2.5 hours. In contrast, the light-adaptational response of *Palaemonetes* lasted 1.5-2 hours and the dark-adaptational response at least five hours.

Evidently, therefore, the dark-adapting hormone persists in the blood until the light-adapting substance disappears and is then able to function. Interestingly, the method whereby the dark-adapting hormone was demonstrated in *Palaemonetes* by Fingerman, Lowe, and Sundararaj (1959b) is applicable to crayfishes. This simple method may ultimately prove applicable to a wide variety of crustaceans.

Fingerman (1957b) studied the endocrine control of the dark red chromatophores of *Cambarellus*. He found that the circumesophageal connectives contained more red pigment dispersing and concentrating substances than did the supraesophageal ganglia. The reverse was true of the distribution of retinal pigment hormones in these organs of *Cambarellus* (Figure 3).

The results presented in Figure 5 revealed that a source of hormone controlling the distal retinal pigment was influenced by long-term adaptation. These results may be compared with those obtained by Fingerman and Lowe (1957b) in a study of the long-term effects of background adaptation upon the chromatophore system of *Cambarellus*. The amounts of red pigment concentrating and dispersing hormones in the circumesophageal connectives changed during a two-week period that the crayfish were kept on the two backgrounds relative to the amounts in the circumesophageal connectives of crayfish that had been on the same shade of background for two hours. The hormone not needed for proper adaptation to one of the backgrounds, *e.g.*, red pigment dispersing hormone of crayfish on a white background whose red pigment was maximally concentrated, increased in the circumesophageal connectives. In the case of the retinal pigments, the amount of light-adapting hormone in the supraesophageal ganglia was different in specimens kept in darkness and under illumination for 17 days.

In Figure 3 are shown the results obtained with extracts of the supraesophageal ganglia of freshly collected *Cambarellus* and in Figure 5 the results obtained with supraesophageal ganglia of specimens that had been kept for 17 days in darkness and under constant illumination. No statistically significant difference was found between the curves depicting the amount of light-adapting hormone in the supraesophageal ganglia of specimens kept in darkness for 17 days and of freshly collected crayfish, whereas the supraesophageal ganglia of specimens that had been illuminated for 17 days contained much less light-adapting hormone than the supraesophageal ganglia of specimens taken directly from the stock aquaria. Presumably the illuminated crayfish were continually secreting light-adapting hormone and were gradually depleting the supply that was available to them at the start of the experiment. These data provide the first evidence for a normal role of light-adapting hormone produced outside the eyestalk in regulation of migration of the distal retinal pigment in any crustacean.

Summary and Conclusions

1. The distal retinal pigment of the crayfish *Cambarellus shufeldti* is controlled by light-adapting and dark-adapting hormones. The former is present in the sinus gland and central nervous organs. The latter can be demonstrated conclusively only in central nervous organs. These hormones are also found in the optic ganglia and supraesophageal ganglia of the crayfish *Orconectes clypeatus*.

2. The presence of both hormones in tissue extracts can be demonstrated by injection into specimens maintained under such an intensity of illumination that the distal retinal pigment is in a condition intermediate between the fully light-adapted and dark-adapted positions. The light-adapting effect precedes the dark-adapted one.

3. The supraesophageal ganglia of specimens of *Cambarellus* illuminated for 17 days contained less light-adapting hormone than the supraesophageal ganglia of specimens kept in darkness for 17 days or of freshly collected specimens. Presumably the animals in light depleted their supply of this hormone. This difference between the animals maintained in light and in darkness is evidence that a retinal pigment hormone outside the eyestalk is physiologically involved in regulation of the distal retinal pigment.

4. The results were discussed in relation to pertinent information concerning the regulation of pigment cells in crayfishes.

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Taxonomic Studies on the Hydras of North America VII. Description of Chlorohydra hadleyi, new species, with a Key to the North American Species of Hydras

HELEN FORREST
Rutgers University, Newark College of Arts and Sciences
Newark 2, New Jersey

INTRODUCTION

The use of hydra as an experimental animal in studies of growth, regeneration and biochemistry has made the identification of hydra species increasingly important. The results of an investigation concerned with one species should not be extended to other species without additional investigation. Unfortunately the identification of hydras to species is difficult and requires exact determination of a constellation of characters.

Green hydras have been known for over 200 years. They are widely distributed in the world, and have hitherto been supposed identical merely on the basis of the presence of zoochlorellae, although a few workers on hydra taxonomy questioned this procedure. European specimens were first named *Hydra viridissima* by Pallas (1766), which name has priority over *Hydra viridis* (Linnaeus, 1767). Marshall (1882) described a form from brackish water, *Hydra viridis bakeri,* characterized by a maximum column length of 1.5 mm for budding individuals, and tentacles half the length of the column. He mentioned several "races" of green hydra and called attention to the great discrepancies in size and proportions of green hydras described by earlier workers (Rösel, Pallas, Kästner, and Schäffer). Schäffer had reported a green hydra with a column length of 1 1/2 inches (37.5 mm), and had observed a small long-tentacled form and a large short-tentacled form, with up to 20 tentacles. Schulze (1917) figured the embryonic theca and testis of European *Chlorohydra viridissima* (placed by him in a separate genus), and suggested that there might be more than one species of green hydra in Europe. This partial description by Schulze, with a few additional comments and a figure of the holotrichous isorhiza in a later paper (Schulze, 1927), until recently constituted the principal characterization of *Chlorohydra viridissima* available for taxonomic purposes. Hyman (1929) called attention to the lack of a complete description of the common green hydra of Europe, and to the resulting uncertainty that all green hydras throughout the world are conspecific. The necessary information about the European green hydra has now been supplied by the beautifully illustrated article by Brien and Reniers-Decoen (1950),

and by the exact scale drawings of its nematocysts by Semal-Van Gansen (1954)—except that no details are furnished in these articles in regard to the embryonic theca.

Detailed studies of green hydras from the eastern United States, mainly New Jersey, have revealed a distinct species which differs in several respects, but particularly in the embryonic theca, from the available descriptions of *Chlorohydra viridissima*. This hydra is named *C. hadleyi* in honor of my former teacher, Dr. Charles E. Hadley, in recognition of his inspiring teaching of invertebrate zoology. The generous assistance of Dr. Libbie Hyman in the preparation of this manuscript is gratefully acknowledged.

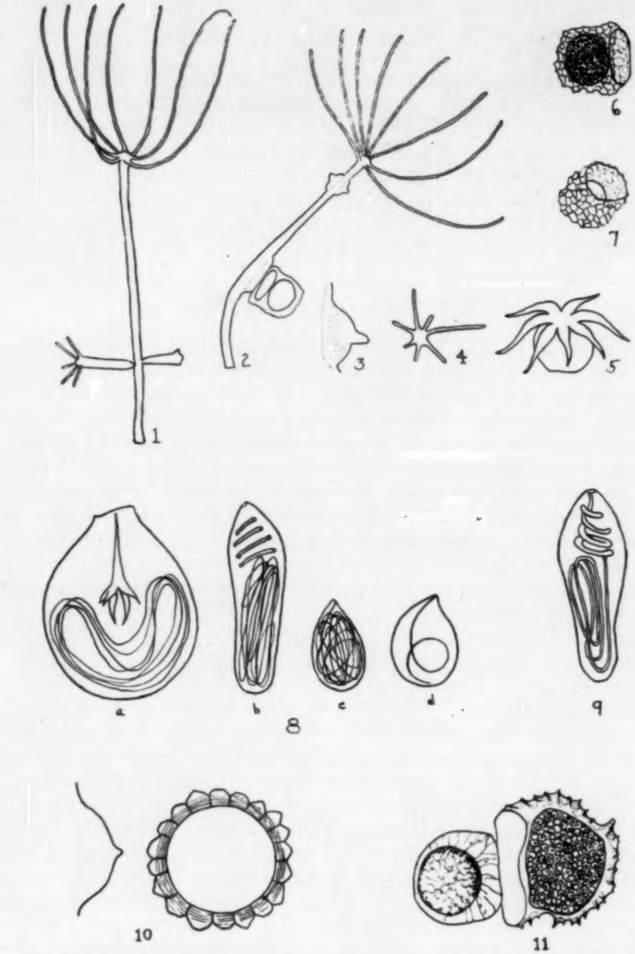
MATERIALS AND METHODS

Living material was used for all measurements and observations. Hydra cultures were maintained in finger bowls of fresh spring water. These cultures were kept throughout the sexual season (May and June) for several years. Small *Daphnia* and pieces of living annelids (*Dero*) served as food. Fresh collections were made at frequent intervals for comparison with laboratory cultures. Nematocyst measurements were made with the use of an ocular micrometer and an oil immersion objective. Whole mounts of sexual individuals were prepared by fixing living hydras in hot Bouin's fluid and staining with borax carmine or Ehrlich's hematoxylin and eosin. Sexual individuals bearing thecated embryos were fixed in hot Bouin's fluid, embedded in paraffin and sectioned.

Chlorohydra hadleyi, new species

General characters.—*Chlorohydra hadleyi* is a small, slender hydra, bright green in color, with short, slender tentacles held somewhat stiffly erect (Fig.1). The most common column length for budding individuals is 7.0 to 7.5 mm. The largest individual collected had, when fully extended, a column length of 13 mm. Sexual individuals remain slightly contracted and range from 2.0 to 8.5 mm in column length, most often measuring about 5 mm. The column may be held erect or slightly curved. Sexual individuals are often bent in the region of the ovaries (Fig. 2). There is no obvious differentiation of a more slender basal stalk region.

The tentacles are always shorter than the column, usually measuring one-half to two-thirds the column length. They are typically held radiating in an upward curve (Figs. 1, 2). Occasionally the tentacle ends droop slightly. More than half of the individuals examined had eight tentacles, and most of the remainder had seven. The largest number of tentacles found on one individual was eleven. Table I shows the distribution of tentacle number in three collections from the type locality in the sexual season, and also gives the number of testes and the occurrence of ovaries.



Figs. 1-8.—*Chlorohydra hadleyi.* 1. Asexual individual with two buds, from life. 2. Typical sexual individual with two testes and one firmly attached embryo, outlined to show the two-chambered theca. 3. Camera lucida drawing of testis. 4. Oral view of bud, showing gradation in length of tentacles. 5. Fully contracted specimen. 6. Lateral view of theca, showing rugose surface, clear proximal chamber, and embryo in distal chamber. 7. Detached theca, oblique view of proximal side. 8. Nematocysts to scale ×3000: a, stenotele; b, holotrichous isorhiza; c, atrichous isorhiza; d, desmoneme. 9-10—*Chlorohydra viridissima.* 9. Holotrichous isorhiza, after Schulze, 1927. 10. Outline of

The bright green color is modified by the presence of a variable amount of brown pigment in the form of coarse granular inclusions within the cells of the gastrodermis. The pigment is most concentrated in the gastrodermal cells underlying the sex organs.

Budding.—Buds appear on both sexual and asexual individuals. They occur singly or in approximately opposite pairs, with the younger bud slightly more distal in position (Fig. 1). In all cases observed, the older bud detached before the appearance of a third bud on the same parent.

Tentacle origin on buds.—Tentacles arise successively on buds. Very young buds show only one tentacle protuberance. Slightly older buds often have six or seven knoblike tentacles, with one a little longer than the others. Some buds show a definite gradation in length among the developing tentacles (Fig. 4), but there is no consistent pattern of tentacle development on buds. Buds usually have fewer tentacles than the parents to which they are attached; additional tentacles develop after the bud leaves the parent.

Nematocysts.—The nematocysts are smaller than those of most hydras. The holotrichous isorhizas and most of the stenoteles are of about the same length, 9.0μ, and most of the isorhizas and desmonemes are about half as long (Fig. 8). The stenoteles range in length from 6.75 to 12.15μ, being mostly about 9.0 to 9.5μ in length. Their width is about four-fifths their length. The holotrichous isorhizas are somewhat slipper-shaped (Fig. 8b) and range in length from 8.25 to 9.75μ, hence are of about the same length as the stenoteles. The thread within the holotrichs has a thickened initial portion that makes three or four horizontal or oblique coils (Fig. 8b), then decreases in diameter and fills the rest of the nematocyst with densely packed longitudinal coils. The atrichous isorhizas (Fig. 8c) are filled with

TABLE I.—Tentacle number and occurrence of testes and ovaries in three groups of *Chlorohydra hadleyi* collected from the type locality in the sexual season

	Tentacle number										Testes				Ovaries
	2	3	4	5	6	7	8	9	10	11	1	2	3	4	
May 14, 1951 19 hydras	..	..	..	..	1	4	14	..	..	..	2	16	1	..	18
May 29, 1952 56 hydras	1	..	1	..	2	16	24	7	3	1	1	48	4	1	52
May 15, 1957 205 hydras	..	..	3	2	10	65	97	23	4	1	2	188	8	1	198

testis and optical section of embryonic theca, after Schulze, 1917. 11—*Chlorohydra hadleyi.* Transverse section through parent column with attached thecated embryo, camera lucida from slide.

a fine thread wound irregularly; they range in length from 4.0 to 4.5μ, with the width about half the length. The desmonemes (Fig. 8d) range from 3.75 to 4.5μ in length, and are almost as broad.

The holotrichs are not as slipper shaped as represented for the European green hydra by Schulze (1927), whose figure is reproduced in Figure 9. However, they agree reasonably well in form with the figure in Semal-Van Gansen (1954).

Sex organs.—This species is hermaphroditic but not at all protandrous. It is unusual among hydras in three respects: 1) almost every individual develops ovaries and testes simultaneously; 2) almost invariably each hydra extrudes but one egg during the sexual season; 3) the thecated embryo remains attached to the parent for two weeks or more. Table I gives the sexual condition of all the individuals in three series collected at random at the height of the sexual season. Of 300 individuals observed to extrude eggs in the laboratory, two eventually bore two embryos and one bore three; all the others developed but one embryo apiece. No individual was found with more than one attached thecated embryo at the time of collection.

Most of the sexual specimens had two mammiform testes with distinct nipples, borne oppositely just below the hypostome (Figs. 2, 3). Ovaries usually appear just above the budding zone (Fig. 2) but are sometimes located more distally.

Period of sexual activity.—At the type locality gonads began to form at the end of the first week in May. Testes and ovaries were conspicuous by the middle of May, and the first eggs were extruded at the end of the third week of May. By the end of the first week in June most of the hydras bore mature embryos and the testes were shrinking. No new embryos developed after the middle of June. Animals collected during May and June and kept under laboratory conditions paralleled the sexual development of those that remained under natural conditions. Individuals from other sources in New Jersey were never found in sexual condition in nature and developed sex organs only in laboratory culture. The factors that induce sexuality in this species have not been determined.

Embryonic theca.—The most distinctive character of this hydra is its embryonic theca, which is divided into two chambers (Figs. 2, 6, 11). The larger distal chamber contains the embryo, which is always flattened to some degree and compressed into the chamber. The more shallow proximal chamber contains a clear fluid. The occurrence of a proximal chamber, unknown in other hydras, is undoubtedly related to the prolonged attachment of the embryo to the parent. The flexible proximal wall of this chamber makes possible a firm attachment to the active parent column, while the fluid-filled cavity provides mechanical protection to the embryo beneath this thin area of the theca. It is also conceivable that the fluid in the proximal chamber might contain dissolved nutrients. All of the 300 or more thecae examined plainly showed the two-chambered construction. The clear proximal chamber could be seen with a 7x hand lens.

When first extruded the egg is smooth, white and spherical. In a day or two it develops a thick, irregular theca. The proximal wall of the theca is flattened, and consists of a smooth, pale yellow, flexible membrane, bounding the proximal chamber. The remainder of the theca is a thick, rigid, thimble-shaped shell, of a light brown material. Its surface is raised in irregular ridges, giving a rugose appearance (Figs. 6, 7). This shell is thicker distally than along its sides. The entire theca measures 350 to 550μ in its largest diameter. The thickness of the wall of the distal chamber varies from 30 to 80μ. The embryo itself measures 250 to 350μ in its largest diameter.

Structural details of the theca are evident in living material but are most clearly seen in sections (Fig. 11). The section of the parent column on the left side of Figure 11 shows the parental epidermis still thickened and closely adherent, over a considerable area, to the thin proximal wall of the proximal chamber of the theca.

Differential diagnosis.—*Chlorohydra hadleyi* is unique among hydras in the possession of a two-chambered embryonic theca. For comparison with the European *C. viridissima* there is available the material in the articles of Schulze (1914, 1917, 1922, 1927, 1931), Brien and Reniers-Decoen (1950), and Semal-Van Gansen (1954). Schulze gave drawings of the holotrich, the testis and the embryonic theca, and these are reproduced here in Figures 9 and 10. Schulze also noted the characteristic slipper shape of the holotrichs and described the testis as mammiform and the embryonic theca as spherical and covered with five- or six-sided, closely set prisms appearing as polygons in surface aspect. The green hydras studied by Brien and Reniers-Decoen were much larger than the present species, attaining a column length of 12 to 30 mm; they produced up to ten testes and as many as seven successive eggs that detached from the parent in about two days. When extruded, the eggs had a greenish tint, which deepened during cleavage. These authors did not describe the embryonic theca, but their figures show it as spherical and thin-walled, of slightly irregular contour, but without projections, hence not consistent with Schulze's account and drawings. The nematocysts of this European green hydra, carefully drawn to scale by Semal-Van Gansen, differ little in shape but significantly in dimensions from those of the present species. It thus appears certain that *C. hadleyi* cannot be identical with the common green hydra of central Europe.

Holotype.—One sexual specimen mounted on slide; also other whole mounts and cross sections through the theca deposited in the invertebrate section of the American Museum of Natural History (*A.M.N.H. No.* 3365).

Habitat and distribution.—The type locality is Lake Wapalanne, Stokes Forest, Sussex County, New Jersey, where this hydra was first found in May, 1951, in a roadside ditch receiving a trickle from a spring. Individuals were found clinging to the undersides of fallen leaves in two or three inches of cool, slowly moving water. For several years collections were made from this source. In addition,

green hydras from other parts of New Jersey (South Orange, West Orange, Upper Montclair, Bloomfield, West Caldwell, Clifton, Little Falls) were cultured and found identical in all respects with the original stock. These hydras have invariably been found in clear cool water in the vicinity of a spring, usually on the undersides of fallen leaves or clinging to the submerged stems of water plants, but sometimes attached to the lower parts of stones or to the undersides of sticks, boards, or pieces of broken glass. They have been collected at all seasons of the year, but have seemed most abundant during spring and early summer. Sexual green hydras from Swarthmore, Pennsylvania, mounted whole on a slide and lent by Dr. Hyman, also proved to be *C. hadleyi.*

DISCUSSION

Comparisons with descriptions of green hydras from other parts of the world are of small value because of the incomplete descriptions. References to such descriptions of green hydras are given in the literature citations (Cernosvitov, 1935; Cordero, 1939, 1941a, 1941b).

The validity of the genus *Chlorohydra* is open to question. This genus is based solely on the presence of symbiotic zoochlorellae in the gastrodermis. Goetsch (1924) artificially inoculated *Hydra attenuata* with zoochlorellae, and Schulze (1927) found specimens of this species with naturally occurring zoochlorellae. Green hydras may be deprived of their zoochlorellae by treatment with glycerine and may then be successfully cultured without them (Whitney, 1907, 1908). Ewer (1948) considered the retention of the genus *Chlorohydra* justified on the ground that the embryonic theca differs so much from that of other members of the Hydridae. This ground becomes doubtful because the theca of the present species differs not only from Schulze's figure but also from that of any other member of the Hydridae. Hence it is not possible to define *Chlorohydra* on the basis of the theca. The presence of symbiotic algae cannot in itself be regarded as of taxonomic value. Although the genus *Chlorohydra* should probably lapse, it is retained here pending further study.

KEY TO THE DESCRIBED SPECIES OF NORTH AMERICAN HYDRAS

1	Tentacles longer than column	2
	Tentacles shorter than column	9
2 (1)	Tentacles three or more times column length	3
	Tentacles up to one and one-half times column length	6
3 (2)	Column distinctly differentiated into body and stalk	4
	Column not distinctly differentiated into body and stalk	5
4 (3)	Holotrichous isorhizas navy-bean-shaped, with all contained coils longitudinal: *Hydra oligactis* Pallas, 1766. Description in Hyman, 1930.	
	Holotrichous isorhizas oval, with four or five oblique coils, the remainder wound longitudinally: *Hydra pseudoligactis* (Hyman, 1931).	
5 (3)	Column up to 17 mm in length, tentacles up to five times the column length: *Hydra canadensis* Rowan, 1930.	

Column up to 20 mm in length, tentacles up to three times the column length, atrichous isorhizas with all coils transversely wound: *Hydra oregona* Griffin and Peters, 1939.

6 (2) Hermaphroditic 7
Dioecious 8

7 (6) Holotrichous isorhizas broadly oval, testes club-shaped, embryonic theca attached and helmet shaped: *Hydra utahensis* Hyman, 1931.
Holotrichous isorhizas narrowly oval, testes mammiform, embryonic theca spherical and spined: *Hydra carnea* L. Agassiz, 1850. Description in Hyman, 1931a.

8 (6) Column slightly differentiated into body and stalk, embryotheca spherical with short broad spines: *Hydra cauliculata* Hyman, 1938.
Column not differentiated into body and stalk, habitat often running water, testes unusually large and with long stout nipples, embryotheca spherical with long spines: *Hydra littoralis* Hyman, 1931. Description in Hyman, 1931b and 1938.

9 (1) Hermaphroditic, embryonic theca attached and bearing small spines: *Hydra hymanae* Hadley and Forrest, 1948.
Usually dioecious, embryotheca spherical with long spines: *Hydra americana* Hyman, 1929.

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Observations on the Nesting Behavior of Digger Wasps of the Genus Ammophila

HOWARD E. EVANS
Cornell University, Ithaca, New York

In the course of studies on the behavior of various digger wasps, I have from time to time made a few notes on various species of *Ammophila* (tribe Ammophilini of the subfamily Sphecinae, family Sphecidae). My reasons for publishing these rather fragmentary notes at this time are two. First, I have been much impressed by the variation in nesting behavior which occurs in this genus, both interspecifically and intraspecifically, suggesting that an intensive comparative study of these wasps might yield important results in the field of the evolution of behavior. Second, I would like to re-examine the idea that wasps of this genus sometimes "use a tool" to assist them in closing their nests. The Peckhams (1898) first reported this behavior in *Ammophila urnaria* and considered it an act of intelligence. Many subsequent writers have not hesitated to cite this behavior as evidence of true intelligence in wasps (e.g., Bouvier, 1918; McDougall, 1923; Hingston, 1929). Recent authors have tended to reject the idea of intelligence and to attach much less significance to the Peckhams' observations (e.g., Frisch, 1940; Baerends, 1941; Thorpe, 1956). Nevertheless the subject still fascinates, and the Peckhams' account still makes its appearance, in one form or another, in many popular books (e.g., Cheesman, 1952; Ley, 1955; Hutchins, 1957). Some writers are apparently unaware that there is now a considerable literature on the subject. My own ideas are summarized at the end of this paper.

Most of the specimens of *Ammophila* which I have studied were identified by myself, but wherever there was any question at all on the identity, specimens were submitted either to K. V. Krombein or to W. D. Murray. The lepidopterous larvae taken as prey were identified by J. G. Franclemont (Noctuoidea), W. C. McGuffin (Geometridae), and H. W. Capps (other groups). The dipterous parasites were identified by C. W. Sabrosky and W. L. Downes, Jr. Some of the observations reported for *procera, harti,* and *urnaria* were made by C. S. Lin and C. M. Yoshimoto. I wish to express my thanks to all of these persons for the assistance rendered.

General Remarks on Ammophila

Probably more has been written on the hunting and nesting behavior of *Ammophila* than has been written about any other genus of digger wasps. Fabre (1879-91) devoted parts of three volumes of his

"Souvenirs Entomologique" to these wasps, and many other European workers have published on them since. The work of Baerends on *"Ammophila campestris"* (1941) has become a classic in the field. Adriaanse (1943) demonstrated that *"campestris"* was, ethologically, two species, and that Baerends' observations were actually made on his "B-form," subsequently described as *adriaansei* Wilcke but later shown to be identical with Curtis' *pubescens* (Richards, 1946). Unfortunately most references to Baerends' work still call the species *campestris,* although this name properly belongs to a species more common farther south, the subject of studies by Grandi and others. Be that as it may Baerends' work is without rival in the field, and there has been no better demonstration of the value of ethological studies in taxonomy than the work of Adriaanse.

Studies of the American species have lagged far behind those on the Palaearctic species. Although the literature is fairly extensive, most of it consists of short notes or of lengthy speculations made from a few observations. I believe the time has come to cut away the shrubbery of speculation and to try to lay the groundwork for a serious comparative study of the American members of this genus. Over 30 species occur in America north of Mexico, and many of the species are common enough to provide excellent material for detailed field studies. I have found the species of *Ammophila* unusually easy to work with; they are large, mild-tempered, and almost impossible to disturb permanently once they are in the process of digging, stocking, or closing a nest.

Ammophila is one of two genera of the tribe Ammophilini. The other genus, *Podalonia,* is in some ways more primitive structurally, and is strikingly more primitive ethologically in that the nest is constructed only after a caterpillar has been paralyzed (in the manner of most Pompilidae). The species of *Ammophila* dig the nest first, close it temporarily, then obtain one or more caterpillars with which to stock it. The majority of species practice mass provisioning, that is, they place the full complement of caterpillars in the cell within a short period, then close the nest permanently and prepare a new one. Others provision progressively, making the final closure only after the larva is quite large; some of these species (*pubescens,* at least) maintain more than one nest at a time. In a sense the Ammophilini are a microcosm of much of the behavioral evolution of family Sphecidae; however, none of the species make multicellular nests or nest elsewhere than in the soil.

The egg is laid on the side of the abdomen of (usually) the first caterpillar placed in the nest. Its upper end is closely fastened to the integument, and the larva begins to feed through the integument at this point of attachment. With its long "neck" the wasp larva reaches around inside the body of the caterpillar and completely hollows it out, leaving the head capsule and the more or less intact body integument. The egg stage usually takes about two days, the larval stage about five days. The larvae of several North American species

have been described by Evans and Lin (1956) and by Evans (1959). The cocoon of *procera* has been described by Krombein (1955).

ACCOUNTS OF INDIVIDUAL SPECIES

In the accounts which follow, I have occasionally made direct reference to my field notes, citing the notes by number. These notes, and accompanying specimens of wasps, prey, and parasites, have been placed on permanent file at Cornell University. A brief review of published observations on each species follows the account of my own observations. I do not pretend that these reviews are complete or that I have done full justice to the work of previous authors. The time is not yet at hand for a comprehensive review of the ethology of all the American species.

Ammophila procera Dahlbom

I have observed one aspect or another of the nesting behavior of this widely distributed species 30 times; 29 of these observations were made in two localities in Pottawatomie Co., Kansas, the remaining one at Ithaca, N. Y. In my experience, *procera* prefers small, flat sandy areas not far removed from trees. The nests are dug in sand which is fairly compact but not overly coarse or hard-packed. Hunting is done in trees well above the ground, and the caterpillars taken are tree inhabiting forms.

My first acquaintance with *procera* was on June 13, 1952, at Blackjack Creek, near Manhattan, Kansas (note no. 51). A female walked into a bare strip of sand along the edge of a cornfield. She was carrying a large caterpillar (*Nadata gibbosa* Smith), holding it with her mandibles on the ventral side behind the hind legs; the caterpillar was venter-up, head-forward, and for the most part did not drag on the ground. The abdomen of the wasp moved up and down rhythmically as she walked along rapidly. The wasp was later found to weigh .18 grams, the caterpillar 1.08 grams, six times as much as the wasp. Once the wasp left the caterpillar briefly as she explored ahead; then she returned and carried it the last 5 meters directly to her nest. She deposited it on the ground, opened her nest by removing several small clods of earth with her mandibles, then entered the nest backward and dragged the caterpillar in behind her. In only a few seconds she reappeared and began to search about for lumps of earth, which she would pick up with her mandibles and either reject or carry into the burrow, depending, I suppose, on their size and consistency. The lumps were placed near the bottom of the burrow and she scraped sand over them. When the burrow was nearly full she took a small lump of earth and ground it down into the burrow with her mandibles. She also packed the earth in the burrow with the ventral part of her head, with her mandibles spread widely. Then she scuffed a little sand over the top and departed.

The nest was dug out and found to be oblique, reaching a depth

of 8 cm and terminating in a horizontal cell 3 cm long and 1.5 cm high. The egg of the wasp, about 3.5 mm long, was laid on the side of the second abdominal segment of the caterpillar, which was well paralyzed. The egg hatched in a rearing tin in two days, and the larva grew steadily for five days, when it began to spin its cocoon. An adult male emerged from this cocoon July 15, 26 days after the spinning of the cocoon.

Digging of the nest was observed in the same area a few days later (June 17; note no. 67). The wasp bit off chunks of soil with her mandibles, forming a small ball of earth between her mouthparts and her front legs. She then flew off about 30 cm, about 10 cm high, and dropped the pellet on the ground. This was repeated many times, rather rapidly, much of the soil being deposited in the same small area. When the nest was completed, she selected several small chunks of earth to close off the entrance, then scraped a little sand over the top.

Subsequent observations confirmed various points and added many details on individual variation. One wasp (no. HE72), in the same area, carried the sand from her nest rather than flying with it, leaving the sand all in a small pile about 15 cm from the nest. All others observed flew with the soil. The temporary closure of the nest usually consisted of several clods of earth, but some used bits of leaves or sand burs; one individual (no. CL24) used a single acorn and another (no. 471) a single rabbit dropping. In making the final closure, one individual used two sand burs and a piece of dried leaf (no. 122), another several pebbles (no. 1474). In some cases some of the same objects had been used for the temporary closure. In searching for objects with which to close the nest, wasps would sometimes go several meters away from the nest. If an object was placed in the burrow and found to be unsuitable, it would be removed and often carried away from the burrow a distance of several centimeters and discarded.

Details of the final closure varied from individual to individual, but always followed the same pattern: solid objects to close lumen of burrow, sand to fill burrow, sand or lumps of earth packed into the top of the filled burrow, sand scraped over the top. When packing, the mandibles are parted and the head moves up and down vigorously; at the same time a loud buzzing noise is emitted. In no instance did I see a wasp actually hold a pebble in her mandibles while packing, although one wasp appeared to lift each pebble up and place it down again several times before finally leaving it in the burrow (no. 1474).

Nineteen nests were dug out. The burrow was found to be usually oblique but sometimes vertical; in a few cases the burrow entered the soil obliquely and then became nearly horizontal. Cell depth varied from 1.5 to 10 cm, with most cells between 7 and 10 cm (avg. 7.2 cm). One unusual nest (no. 320) is not included in these figures. This wasp spent considerable time circling about with her caterpillar before finally dragging it into what appeared to be a

burrow of *Bembix belfragei* Cresson. After a moment the wasp emerged and selected several bits of earth and horse dung to close the burrow; she then proceeded to make a final closure in the usual manner, but did not level off the pile of sand at the entrance which the *Bembix* had left. This burrow was found to reach a depth of 23 cm, but the closure occupied less than half of the burrow, the lower part being left open. Almost certainly, this *Ammophila* had mistaken the *Bembix* burrow for her own.

Every nest dug out contained only a single caterpillar. The egg was found to be laid on the second abdominal segment in four instances, on the third in ten instances, and on the fourth in three instances. All caterpillars belonged to the family Notodontidae with the exception of one noctuid which could not be identified further (no. L57). Fifteen of the notodontids were identified by J. G. Franclemont as follows: *Nadata gibbosa* Smith—12; *Heterocampa manteo* Doubleday—1; *Schizura ipomoeae* Doubleday—1; *Symmerista* sp.—1. *Nadata gibbosa* was used as prey both in Kansas and at Ithaca, N. Y.; it is an oak feeder.

None of the nests in the Kansas localities were parasitized, although in one instance (no. HE72) a small fly was observed near a wasp which was digging a new nest; this fly was attacked by the wasp and driven away. At Ithaca, N. Y., a fly was seen lurking about a nest during the final closure (no. 1474). When this nest was dug out two days later the egg of the wasp had disappeared and six small maggots were feeding on the caterpillar. These maggots reached a large size in two more days and shortly thereafter formed their puparia in the soil beneath the cell (Aug. 2). The following April a single *Senotainia vigilans* Allen emerged from one of these puparia.

The several published observations on this species can be reviewed only briefly. Pergande (1892) observed a female piling pebbles over the top of a filled nest; this nest was dug out and found to contain a single *Heterocampa subalbicans* Grote (=*manteo* Doubleday) (Notodontidae) bearing the wasp egg. The more detailed observations of Hartman (1905) are provided with excellent photographs. Hartman reports that the earth is carried from the burrow over the ground and deposited a short distance away. Larger individuals, he states, use a single caterpillar per nest, in this case a tomato hornworm (Sphingidae), while smaller individuals use several caterpillars per nest.[1] The egg is laid at any point from the third to the seventh abdominal segment. The final closure is made by placing bits of debris in the burrow and "scratching in . . . sand . . . and tamping it down with her head. When the nest is full enough for the wasp to reach down comfortably she presses the pieces firmly down before

[1] This remark leads me to believe that Hartman may have been confusing more than one species under the name *procera*. The size variation in *procera* is not unusual, and no one else has ever observed the species employing more than one caterpillar per nest. Misidentifications are not uncommon in Hartman's paper.

she lets go. . . . It sometimes happens . . . that a piece of wood is pressed down tightly, then pulled out and pressed down again and this repeated several times, so that one might suspect that the wasp were here improvising a tool with which to tamp down the sand."

The "use of a tool" by this species has also been reported by G. C. and E. H. Wheeler (1924), who saw a wasp in northeastern Texas "tamping down filling with a pebble," the body held vertically, "like a pile-driver." I am not aware that any other workers have noted this behavior in *procera*.

Criddle (1924) found this species preying upon Sphingidae in Manitoba. Of four individuals he watched, three flew with the soil during digging and one ran with it. He noted that during closure the soil is packed with the head and stones are pressed into place in the burrow. Rau (1918, 1922, 1926) on two different occasions saw this species flying with soil from the nest; he reported *Nadata gibbosa* (Notodontidae) as prey and also a noctuid caterpillar. Bohart and Knowlton (1953) also report that this species flies with the soil, "flinging it away with a quick turn of their entire body"; they report Notodontidae as prey, nest depth as 8 inches.

The most extensive recent studies are those of Krombein (1953, 1955, 1958). Krombein reports several species of Notodontidae as prey, only one caterpillar being used per nest. The egg is laid on the side of either the third or fourth abdominal segment. He reports that the soil removed from the burrow is carried on the wing a distance of 6 to 9 inches from the entrance. Filling consists of sand interspersed with debris. He found the nest depth to vary from 3 to 6 cm. In general, Krombein's observations agree very closely with my own.

Ammophila aberti Haldeman

This species is widely distributed in the western half of the United States. I have observed it nesting once in Grant Co., Kansas, Aug. 18, 1952, and five times on the beach of Laguna Madre, near Port Isabel, Texas, May 8-11, 1958. The species appears to be characteristic of open, semi-arid country, nesting chiefly in firm sand not far from water.

The one individual observed in western Kansas was making a final closure of a nest in flat soil not far from the banks of the Cimarron River (note No. HE106). The wasp picked up a small pebble about five meters from the nest, flew to the nest with it, and pounded the earth in the nest entrance, holding the pebble in the mandibles. Whether the pebble was discarded or used for fill was not noted. She then scraped some sand over the top of the nest entrance. This nest was dug out and found to be oblique, terminating in a cell at a depth of 8 cm. The cell contained 10 caterpillars, all apparently a single species of Geometridae of the subfamily Sterrhinae. Three of the caterpillars appeared to be fresh, but the other seven showed signs of deterioration. The egg was in poor condition and the cell contained

several small maggots, not successfully reared but presumably those of a miltogrammine. Thus provisioning of the nest had apparently taken place over several days, and the female continued to provision even though her egg had been destroyed.

In the Texas locality, several individuals were observed during various stages of nesting, and notes were made on five of these. All nests were in bare places on the upper part of the beach, where the soil was very firm. When digging the nest, the female bites off bits of earth (with a loud buzz) and gathers them into lumps which are held between the mandibles and front legs; she then flies off a distance of from 1 to 1.5 meters (about half a meter high) and drops them on the ground. Most of the soil is deposited in the same general area. After the nest is complete, a temporary closure is made by placing one or more solid objects in the lumen of the burrow and scraping sand over them. In this area pieces of shell or bits of the hard surface crust were used for closing off the burrow.

Several individuals were observed carrying caterpillars, and without exception they carried them in flight, although employing the same grasp as in *procera*. The caterpillar is dropped on the threshold of the burrow; the wasp then removes the closure, enters the nest, turns around, and draws in the caterpillar head first. The egg is laid on the first caterpillar placed in the cell. After each caterpillar but the last, the temporary closure is replaced; after the last one a more elaborate final closure is made. The egg is laid laterally between the second and third abdominal segment (2 records) or between the third and fourth segment (1 record). Only one nest was dug after it was fully provisioned (no. 1542); this nest contained 9 caterpillars, all one species of the genus *Euchlaena* (Geometridae). Most of the other nests contained this same geometrid, but two nests each contained one skipper larva of an unknown genus (Hesperiidae). The burrow was found to be either vertical or slightly oblique, reaching a depth of from 5 to 9 cm (avg. 7.1 cm).

Final closure was observed in detail only once (no. 1542). This individual first placed a small piece of leaf near the bottom of the burrow. She then scraped in some sand, went in and pressed it down with her head, reappeared and scraped in more sand, went in and pressed again, and so on until the burrow was full. Finally she picked up a small seed and pounded the earth over the entrance with it; she then scraped a little more sand and pounded again with another seed. Each time the seed was held firmly in the mandibles and later discarded. She next carried several bits of surface crust and placed them over the entrance. Then she picked up a small stick and used it to pound up the crust; finally she discarded the stick and flew off.

When this nest was dug out, it was found to contain nine rather fresh caterpillars, but the egg had been destroyed by maggots, which were already of fair size. This nest is known to have been provisioned over a period of at least two days, and judging from the size of the maggots, oviposition had probably occured three or four days previ-

ously. Thus some measure of progressive provisioning seems to have occurred. All the other nests dug out contained eggs and up to four caterpillars, but none of these had received the final closure.

The maggots were successfully reared and found to be an undescribed species of the genus *Opsidia* (Sarcophagidae, Miltogramminae). This same species was seen flying about the nest entrances of various digger wasps (chiefly *Bembix*), but it was not observed trailing wasps with prey. Presumably it enters the nest for larviposition.

Ammophila aberti was first studied by Williston (1892, under the name *yarrowi*) in western Kansas. Numerous females were found nesting in hard soil and provisioning their nests with four or five small, green larvae. Closure of the nest, even the temporary closure, was reported to include pressing the soil in the burrow with a pebble which was later discarded. Hicks (1932) later studied this species in much greater detail near Boulder, Colorado, where many individuals were nesting in flat, dry, open areas where the soil was relatively hard. He found that the soil taken from the nest is carried in flight a distance of from a few inches to five feet, a given individual depositing most of the soil in one spot. The nest is provisioned with from 5 to 8 geometrid larvae. These may be brought in over a period of up to 7 days, in which case the larva is quite large during the later stages of provisioning; on the other hand, some individuals complete provisioning rapidly, before the egg has hatched. Hicks believed that more than one nest might be maintained at one time. The nest is about 4 cm deep, the cell 3.5 cm long. The egg is, of course, laid on the first caterpillar placed in the cell. Hicks found *aberti* to be attacked by the miltogrammine fly *Hilarella hilarella* (Zett.) and the chrysidid wasp *Chrysis perpulchra* Cresson.

Most of Hicks' paper has to do with the "use of a tool" by this species. He found that females sometimes leave a nest temporarily before finishing it, and even then they make a temporary closure, sometimes pounding the soil in the burrow briefly with a pebble. The closure made between trips for prey is more thorough than this, the final closure still more thorough. Invariably pebbles of a certain size are selected and "used as a hammer." "Sometimes the wasp vibrated it in place between hammer-like strokes." The pebble is sometimes left in the burrow, sometimes discarded. In his many observations, Hicks noted relatively little variation in the manner of closing the nest.

Amnophila placida Smith

I found this species nesting in great numbers May 8-11, 1958, on the beach of Laguna Madre, near Port Isabel, Texas, in exactly the same area as in the preceding species, thus affording an excellent opportunity to compare the two species. Many individuals were observed in various phases of nesting; in fact, one could walk but a short distance along the beach without hearing the characteristic buzz of a

female digging or filling her burrow. Detailed notes were made on 14 individuals.

Most nests were dug in bare places on the beach, well above the high water mark, but a few were dug close to or beneath halophytes growing on the beach. The earth is scooped out with the mandibles and front legs and is ordinarily carried in flight a distance of 30-50 cm, only a few centimeters high, and dropped on the ground. However, one individual (no. 1531), nesting beneath a large clump of vegetaiton, where flight may have been difficult, walked from her nest with the earth. In either case the trips from the nest are in various directions, so that the earth is well scattered. A temporary closure is made by placing one or more solid objects — in this area usually bits of shell — in the lumen of the burrow near the top, and scraping a little sand over them.

Many individuals were seen carrying prey, and in every case the prey was carried over the ground in the same manner as in *procera,* although *placida* uses much smaller caterpillars and lifts them well off the ground. The caterpillars were often carried great distances along the beach. In this area only one species of caterpillar was used, a small green skipper (Hesperiidae) of unknown genus and species (50 caterpillars, taken from 14 nests). The number of caterpillars per completed nest varied from 3 to 5. The egg is laid on the first caterpillar placed in the nest. It was found to be laid on the side between the first and second abdominal segment (5 records), between the second and third segment (1 record), on the side of the third segment (1 record), or between the third and fourth segment (1 record).

The nest is a simple burrow, vertical or nearly so, terminating in a horizontal cell about 2.5 cm long. Cell depth varied, in this area, from 4 to 10 cm (avg. 6.7 cm). Burrow diameter approximated 6 mm. Some individuals, at least, tend to make several successive nests in the same small area. Wasp no. 1531 had apparently prepared three successive nests only about 5 cm apart. Most nests are dug in the morning, provisioned during the day, and given a final closure in the late afternoon. However, some nests were not completely provisioned and closed until the second day.

The final closure of the nest of this species is a most unusual performance and was observed many times. The closure requires about 30 minutes, and during much of this time the wasp buzzes so loudly that she can be heard some distance away. The burrow is first closed off near the bottom with a piece of shell or plant material which is selected from the objects lying about the nest entrance. The wasp then begins to dig a new burrow 1-2 cm away, using the soil from this burrow to fill the original one. The soil is carried in lumps from the new burrow to the old, then packed into place with the head, which is moved up and down rapidly while the wasp emits a loud buzzing sound. When the burrow is completely filled, soil is scuffed in various directions over the top, and in most cases lumps of earth

and bits of twigs and other vegetation are placed over the filled burrow. The new or "false" burrow is left open and abandoned. There was considerable variation in the depth of the false burrow, and, as might be expected, the deeper false burrows invariably were associated with the deeper true burrows. In nests in which the true burrow varied in depth from 4 to 6 cm, the false burrow varied in depth from 1.5 to 3 cm; in nests in which the true burrow was 8 to 10 cm deep, the false burrow was from 4 to 4.5 cm deep. The average depth of the false burrow for all nests in which measurements were taken was 3 cm.

The egg of this species hatches in two days and the larva reaches maturity after about five days of feeding. The caterpillars remain fresh and relatively lively until consumed by the wasp larva. Nearly every nest dug out was found to contain fecal pellets of the caterpillars. One larva which spun its cocoon on May 17 produced an adult on August 16.

Two nests (nos. 1513, 1536), when dug out, were found to contain several maggots which had destroyed the egg of the wasp and begun to feed upon the caterpillars. These maggots were removed to rearing tins and in both cases formed their puparia six days after the nest was provisioned. Puparia from both nests later produced adult miltogrammine flies determined by W. L. Downes as a new species of the genus *Opsidia*. This same species was also reared from nests of *A. aberti* in this area. These flies were not observed following wasps laden with prey; presumably they enter the nests for larviposition.

The published observations on this species were all made in localities farther north, and differ considerably from those made by the present author in southern Texas (although agreeing fairly well among themselves). Walsh and Riley (1869) reported on some observations made in southern Illinois, Rau and Rau (1918) on observations made in Missouri,[2] and Standtmann (1945) on observations made in Ohio. All three reports state that a single caterpillar is used per nest; all three state that cutworms (Noctuidae) are used as prey, although the Raus state that hesperiid and geometrid larvae are occasionally used as well as noctuids. Walsh and Riley and the Raus report that the cutworm is carried over the ground as I have described; Strandtmann did not observe this aspect of the behavior. The Raus and Strandtmann both state that the soil removed from the burrow is carried away from the nest on foot; the Raus state that it is piled in one place, Strandtmann that it is scattered in different places. These authors do not describe a distinct "false burrow," but Walsh and Riley say that their wasp (observations quoted from T. A. E. Holcomb) "commenced digging a second hole. . . about an inch away from the first;

[2] Walsh and Riley and the Raus use the name *pictipennis* Walsh for this species. In the former case there is little doubt that the species referred to is the one now called *placida* Smith, but in the case of the Raus there is a possibility that the species concerned was actually *fernaldi* Murray.

and with the dirt that came out of this she filled up the first hole. . . ." The Raus remark that if the wasp "uses all the loose dirt lying nearby, she. . . simply bites some more loose. . . from the surface of the ground and uses that."

Strandtmann mentions that the wasp picks up small pebbles near the nest and presses them in the burrow. "When the hole was nearly full," he states, "she scratched loose sand into the opening and pressed it down with a small pebble held in her mandibles." He reports that the pebble is sometimes left in place, sometimes removed and used again for further pounding. The Raus discuss at considerable length the "use of a tool" by this species. They observed numerous individuals and found relatively little variation in this behavior. At first the burrow is packed with loose dirt only. When the burrow is still about one-fourth inch deep, the wasp placed a series of clods of earth in the burrow, grinding each into dust. When the burrow is full, a firmer clod or piece of wood is selected, with this "she rubs, pounds and hammers down the dirt on the top of the hole until all traces of the fill are obliterated. When she has finished. . . she throws her tool aside a few inches. . ."

Allen (1926) reports that both J. B. Parker, at Washington, D. C., and M. R. Smith, in Mississippi, found the miltogrammine fly *Hilarella hilarella* (Zett.) attacking "*Sphex extrematata* var. *pictipennis* Walsh," presumably *Ammophila placida*. Both these observers found only one caterpillar to a nest; in the latter case the corn earworm, *Heliothis zeae* (Boddie) (Noctuidae) was used.

Ammophila harti (Fernald)

This species is widely distributed in the eastern two-thirds of North America but appears to be restricted to open sandy areas. Within its range *harti* is the only species of the genus which normally occurs in large sand dunes, where it is found in association with such digger wasps as *Bembix pruinosa* and *Microbembex monodonta*. I have observed the species nesting ten times; all observations were made during the summers of 1952-53 in four localities in central Kansas.

The nest is dug in sand which is flat or sloping. The sand is picked up in small lumps which are carried a distance of 10-15 cm in flight and dropped on the ground, the wasp returning very quickly to the burrow and scooping up another lump of sand. When the burrow is complete, the wasp walks about seeking a lump of sand or a small stone to close off the burrow. In the search for this, she may walk several meters from the nest, her abdomen held high, forming about a 30° angle with the ground. Various small objects are embraced with the mandibles; when one is found of the right size and consistency it is grasped with the mandibles and front legs and carried on foot back to the nest. One individual (no. 120) failed to find her nest on two different occasions, and had to abandon the pebble and fly to her

nest, then find another pebble. After closing off the lumen with one or more pebbles, the wasp scuffs loose sand into the outer part of the burrow to complete the temporary closure.

The nine nests dug out were all oblique, with a burrow 7.5-12 cm long (avg. 9.6 cm) leading to a cell 3.5-10 cm beneath the surface (avg. 7.0 cm). The cell measures about 1 cm in diameter and 2-2.5 cm long. The egg is laid on the first caterpillar placed in the cell. In three instances it was found to be laid on the side of the second abdominal segment, in one instance on the third, and in one instance between the third and the fourth.

The caterpillars used as prey by this species are all small, looper-type caterpillars, often green in color. Of twenty caterpillars taken from various nests or wasps, three were Noctuidae, probably of the subfamily Acontiinae, and the remaining 17 Geometridae, some of the subfamily Ennominae and some of the subfamily Sterrhinae. The caterpillars are carried to the nest in a characteristic manner: they are grasped just behind the head and carried in short flights of from .5 to 2.5 meters, the caterpillar dangling freely from the wasp's mandibles. The pause between each flight is brief, so that the wasp seems to be proceeding by a series of long hops over the sand. The prey is, as usual, left at the threshold of the burrow while the wasp opens the burrow; it is then drawn in headfirst from the inside. The largest number of caterpillars found in any nest was four, but the full complement may sometimes be more than this. Since this species provisions progressively, the first caterpillars have been mostly consumed by the time the last ones are added.

Provisioning apparently extends over several days, and the wasp larva is fairly large by the time the last caterpillar is added. Whether this species provisions more than one nest simultaneously remains to be determined. In several nests (nos. CY92, 390, 484, 502) the female provided one or more fresh caterpillars for a fairly large larva, and in each case the only other caterpillars in the cell were partially or wholly consumed. In each case there had apparently been a gap of at least two or three days since the first provisioning and the final period of provisioning. Surely it would seem possible that the wasps may have started another nest in the meantime.

The final closure of the nest does not appear to differ significantly from a temporary closure; a few pebbles are used to close the lumen of the burrow, and the remainder of the burrow is filled by scuffing in sand. No pounding of the sand in the burrow was observed. No parasites were found in association with any of the nests studied.

The observations of the Peckhams (1900, under the name *polita*) agree closely with mine. They found the species nesting in open sand and preying upon four species of small caterpillars; the caterpillars were carried to the nest in short flights as I have described. They found the burrow to be five inches long, the cell two inches beneath the surface. The nest was provisioned progressively with 5 or 6 caterpillars. Rau (1922) observed this species (under the name *argentata*)

nesting in a sandy area and carrying the sand from the nest on the wing; the prey was found to consist of Geometridae. My report (Evans, 1958) that this species employs mass provisioning is in error.

Ammophila juncea Cresson

Nothing has previously been recorded on the nesting behavior of this widely distributed but relatively uncommon species. I have observed it nesting four times, during the summers of 1952 and 1953, in three different localities in Pottawatomie Co., Kansas. In each instance it nested in a somewhat restricted area of sand in the vicinity of trees. The caterpillars used as prey were tree-dwelling species of the families Notodontidae and Noctuidae. Only one of the caterpillars was actually determined, the others used for rearing larvae; this was identified as *Macrurocampa marthesia* (Cramer), a notodontid which feeds on oak.

The nest is dug in flat sand, often near or beneath herbaceous plants. The sand is carried from the burrow in flight and dropped on the ground about a meter away, most of the sand being dropped in the same general area. A temporary closure is made by placing several small solid objects near the top of the burrow and filling the rest with sand. One wasp (no. HE79), nesting near a railroad track, used four black cinders to close off the burrow; another (no. HE81) used one large lump of earth and two smaller ones.

All four burrows were L-shaped; that is, the burrow was straight or nearly so, leading to a horizontal cell. Cell depth varied from 4 to 6 cm (avg. 4.8 cm); cell length varied from 25 to 35 mm. Three of the four nests had received the final closure when dug out; two of these contained one caterpillar and one contained two. In all four instances the egg was laid on the side of the third abdominal segment; in the nest containing two caterpillars (no. 332) the egg had been laid on the second caterpillar placed in the cell rather than the first. The caterpillar is carried to the nest over the ground in the manner described for *procera*.

Final closure of the nest showed some variation from one individual to another. No. HE79, which had used black cinders in the temporary closure, also used such cinders to block off the burrow in the final closure. She then scraped sand into the burrow until it was nearly full, then added more cinders, putting each in place with a certain amount of pressing, but no pounding. No. HE81, after filling the burrow nearly to the top, picked up a small lump of earth and pounded the sand in the burrow while holding the lump in her mandibles. No. 332 placed a number of lumps of earth in the burrow and ground each of them up by pounding and chopping with her mandibles. In each case the burrow was eventually concealed well by kicking sand over the top in various directions.

One wasp (no. 537) was followed by a small fly which hovered about 5-10 cm behind her as she carried her prey to the burrow. The fly apparently did not larviposit on the prey, as no maggots were found

in the cell when it was dug out. The fly was captured and identified as *Senotainia litoralis* Allen.

Ammophila urnaria urnaria (Dahlbom)

This is the commonest *Ammophila* at Ithaca, New York, where I have observed it nesting eight times. The species is characteristic of open country and nests in gravel pits, waste places, and gardens, often where the soil is fairly firm. The small caterpillars which serve as prey include species which feed in trees as well as species which feed on herbaceous plants, so apparently *urnaria* hunts rather widely. Digging of the nest was observed only once, on June 28, 1954 (note no. 687). This individual began a nest about 3 p.m. and completed it 30 minutes later. The earth was removed from the burrow in small lumps which were carried between the mandibles and front legs, over the ground, and deposited 10-20 cm from the hole, mostly in one small area. The temporary closure of this nest consisted of 5 small pebbles plus a small amount of sand. Other nests appeared to have been closed by only one or two pebbles or lumps of earth.

The caterpillars are carried to the nest in the same manner as in *procera,* although because of the small size of the caterpillars they are usually lifted well off the ground. In one instance (no. 1500) a female was seen to fly a considerable distance with her caterpillar, landing not far from the nest and carrying it over the ground the remaining distance. Most characteristically, the wasp would proceed over the group in nearly a straight line until she arrived in the vicinity of the nest, whereupon she would circle about until finding the nest. No. 1551, which I found after she had just stung a caterpillar in my garden on July 13, 1958, proceeded to the edge of the garden between two rows of peas, then made a right angle turn and followed a furrow for about 4 meters. At this point she made another right angle turn away from the garden and proceeded for one meter through a dense tangle of weeds, where she located her nest without any circling whatever. This was the first return of the wasp to her nest in three days (it had rained continuously the preceding two days, and the nest had obviously not been reopened since the rain). Once at the nest, the wasp deposits the caterpillar a short distance from the entrance, removes the closure, and draws the caterpillar in from the inside.

The number of caterpillars used per nest seems to vary considerably. Two nests which had received the final closure contained only one caterpillar (nos. 1013, 1202); in both cases the caterpillar was a large geometrid of the subfamily Ennominae. Three other nests contained two caterpillars each; no. 671 contained two *Scoliopteryx libatrix* L. (Noctuidae), no. 1551 two *Autographa* sp. (Noctuidae), and no 1119 one *Panopoda* sp. (Noctuidae) and one geometrid larva of the subfamily Ennominae. Another nest (no. 918) contained six small geometrid larvae.

The burrow of this species may be vertical or oblique. Cell depth,

in the nests examined, varied from 2 to 5 cm (avg., 3.7 cm). Cell length varied from 1 to 1.25 cm. The egg is laid on the first caterpillar placed in the nest. In four cases it was found to be laid on the side of the fourth abdominal segment, in two cases on the third, in one case between the third and fourth, and in one case between the second and third.

Although this species mass-provisions its nests, on some occasions provisioning may not be completed until after the egg has hatched. No. 918 placed a caterpillar in the nest and made a final closure on Sept. 9, 1954; this nest was dug out immediately and found to contain two fresh caterpillars and four older ones which had been partially consumed by the half-grown larva. No. 1551, mentioned above as having returned to her nest following two days of rain, placed her second caterpillar in the nest after the egg had already hatched.

Final closure of the nest was observed several times. No. 1013 closed off the lumen of the burrow with a single large lump of earth which she selected from several lying near the nest; she then alternately scraped in soil with the legs and packed it in place with the head, her mandibles open wide. When the burrow was filled she scraped more sand over the top, concealing the nest well. She did very little buzzing, and at no time did she pick up pebbles or lumps of earth other than the first one. No. 1551 behaved somewhat similarly, but on three or four occasions picked up small pebbles, pounded with them, then rejected them. Most of the pounding, however, was done with the head itself, with the mandibles open wide as usual.

The work of the Peckhams (1898) on this species is well known. They found numerous individuals nesting in their garden, taking their caterpillars mostly from among weeds and bean plants. Usually two caterpillars were used per nest, but one nest contained only one large caterpillar. The egg was found to be laid on the side of the third or fourth abdominal segment. They found that mass provisioning is ordinarily employed, but one individual brought in her second caterpillar after the larva was at least a day old. Closure of the nest varied greatly from one individual to another, and one particular wasp picked up "a small pebble in her mandibles and used it as a hammer in pounding"; they claim that this wasp "improvised a tool and made intelligent use of it." These remarks of the Peckhams have been widely quoted, and their sketch has been reproduced in many books.

Parker (1915) also studied this species briefly. He states that the soil dug from the nest is usually carried a short distance on the ground and deposited, but one individual was seen to fly with the soil. The caterpillars are carried over the ground to the nest, but occasional flights of a foot or more may be made. He dug one nest which contained five caterpillars, four small Geometridae and one larger specimen which appears from his photograph to be *Polia adjuncta* Boisduval (Noctuidae). The egg was laid longitudinally on the side of a very slender geometer. The paper of Frisch (1940) is primarily a criticism of the Peckhams' claims regarding this species, but he ap-

parently had made some observations on *urnaria*. He says, for example, that he found a nest with two cells. So far as I know, this is the only report of any species of *Ammophila* making more than one cell per nest.

Ammophila aureonotata Cameron

I have observed this species nesting only once, on the campus of Kansas State College, Manhattan, on July 10, 1942 (note no. HE4). At 1 p.m. I noticed a wasp and its caterpillar struggling on a sidewalk; the caterpillar, a notodontid of the *Heterocampa*-group, may have fallen or been flushed by the wasp from a tree directly overhead. When first seen, the caterpillar was twisting back and forth violently and the wasp was buzzing its wings and applying the tip of its abdomen to various points on the body, presumably stinging it in various places. As the caterpillar became somewhat subdued, the wasp grasped it dorsally and posteriorly with her mandibles and stung it once, much more slowly, between the abdominal prolegs. She then turned around and grasped the caterpillar just behind the head and stung it again between the thoracic legs and again on the venter just behind the head. The caterpillar was by this time completely quiet, and the wasp began to squeeze the thorax with her mandibles and lap up the blood which exuded from the wounds. She did this off and on for 30 minutes, carrying the caterpillar about a meter in the meantime. The caterpillar was carried over the ground in the same manner as in *procera;* the abdomen of the wasp was held high and moved up and down rhythmically. Finally she carried the caterpillar directly to her nest, which was beneath a currant bush about 6 meters away. She placed the prey just outside the burrow while she removed the closure, which consisted of a single dried, wrinkled leaf, then pulled it into the nest from the inside. She then placed several pellets of earth and bits of leaves in the burrow with her mandibles and scraped a little soil into the burrow with her forelegs. The nesting process took only five minutes, and the top of the nest was not smoothed off or covered in any way. The burrow was L-shaped, only 5 cm deep. It was dug out with some difficulty, since the soil was a hard-packed loam and full of roots. The egg was dislodged from the caterpillar during digging.

The Peckhams (1898) reported briefly on two specimens of this species (under the name *gracilis*). One of them carried a large green caterpillar out of a woods and through a garden, covering 261 feet in about two hours, before finally abandoning the prey. The second one dug a nest in a garden, made a temporary closure with bits of cornstalk and pellets of earth, but failed to provision the nest. Rau (1922) reported the species (under the name *abbreviata*) preying upon skipper larvae (Hesperiidae). Krombein (1958) observed an individual carrying a notodontid caterpillar, *Heterocampa guttivitta* (Walker). The caterpillar was deposited at the edge of the burrow while the

wasp removed the temporary closure by flying backwards with the litter and dropping it on the ground. The burrow was filled by scratching in sand and packing it in place with the under side of the head, with the mandibles open. The egg was found to have been laid on the side of the fourth abdominal segment.

Ammophila nigricans Dahlbom

I have on three occasions seen this species at Ithaca with its caterpillar, but in no case did I follow the wasp to its nest. In all three instances the wasp was seen in small sandy areas in the proximity of woodland. The caterpillars used as prey are very large, and as a result the wasp and prey are very conspicuous as they proceed over the ground. No. 713 carried a full-grown larva of *Euparthenos nubilis* Hubner (Noctuidae). The caterpillar was dragged along the ground in the manner of *procera,* but was so large the wasp could barely straddle it. The wasp was 23 mm long and weighed .1 gm; the caterpillar was 43 mm long and weighed 1.3 gm, or 13 times as much as the wasp. No. 1136 also carried a larva of *Euparthenos nubilis.* No. 1560 carried a larva of *Zale* sp. which was nearly 60 mm long; this caterpillar was carried sideways rather than venter-up, probably because the curvature of its long body made the usual manner of carriage very difficult. In all three cases progress was very slow; in no case did the wasp use its wings for propulsion and in no case did the abdomen work up and down rhythmically as sometimes occurs in *procera* and *aureonotata.* Both caterpillars feed on the foliage of trees, the *Euparthenos* on *Robinia,* which grows commonly in sandy soil in the Ithaca area.

Rau (1934) reports that this species constructs an L-shaped burrow only 4 cm deep, each nest containing only one caterpillar. The egg in two instances was found to be laid on the side of the second abdominal segment, in one instance on the third. He states that "two of the caterpillars were encrusted with earth; this indicated that they were subterranean. . ."; apparently they were not actually identified. Strandtmann (1945) found the species preying upon *Catocala* sp. in Ohio and using only one caterpillar per nest. The one nest he dug out had an oblique burrow reaching a depth of only 4 cm. The wasp egg was attached to the second abdominal segment.

Ammophila xanthoptera Cameron

This species has been the subject of an excellent study by Hicks (1932), who found it nesting in the moist, sandy soil of a river bed near Los Angeles, California. The prey consisted mostly of the noctuid *Zale lunata* (Drury), and only one caterpillar was used per nest. The soil is dug from the nest in the usual manner and carried on the ground a short distance from the nest entrance, where it comes to lie

mostly in one small area. The temporary closure consists of a lump of sand plus some loose sand which is scraped over the top. The nest varies from 28 to 65 mm deep, the average about 55 mm. The caterpillar is carried to the nest over the ground and placed in the nest in the usual manner. The egg is laid on the first to the fourth abdominal segment, usually on the second.

A considerable section of Hicks' paper is devoted to a description of the final closure of the nest. Much of the sand for filling the burrow is obtained by digging in one spot, so that a small tunnel is dug much as I have described for *placida*. The sand is spread out in the burrow by the head, with the mandibles opened widely. Toward the end of filling, the wasp selects a small pebble and uses it to pound the sand in the burrow, sometimes discarding the pebble and sometimes leaving it in place. Although much variation was observed in the details of final closure, all wasps made use of one or more pebbles for pounding. In fact, they also did this even when filling up the burrow which had been dug to obtain soil for the true burrow.

Ammophila pruinosa Cresson

Hicks' (1933) observations on *Sphex breviceps* (Smith) probably apply to *pruinosa* Cresson. The latter name is cited as a synonym of *breviceps,* although the two species are now regarded as distinct. He reports that this wasp uses several small moth larvae per nest, "often apparently including many species"; the specimens of prey of *pruinosa* I have seen in collections consist of very small microlepidopterous larvae.

Hicks found that the soil is usually carried from the nest on the wing, although one wasp nesting in midst of grass and debris carried the soil over the ground. The nest is very shallow, only 25 mm to about 60 mm deep. The temporary closure consists of a pebble to close the lumen of the burrow plus some sand scraped over the top. The caterpillars are carried to the nest in flight. Apparently mass provisioning is the rule, although in some nests the egg hatches before provisioning is complete. This species was not observed to pound the soil in the nest entrance either with its head or with a pebble held in its mandibles.

Discussion

The reader will have noted that all species of *Ammophila* appear to exhibit a certain amount of variation in their nesting behavior. In a number of instances (but especially in the case of *placida*), all published observations are not in close agreement with my own. What is needed in this genus is a detailed study of one or more species in different parts of their range in order to determine exactly how much variation does occur among the individuals of a single species and what the nature and significance of this variation is. Until this is done, one must be cautious in his treatment of what appear to be interspecific differences in this genus (see Table I).

TABLE I.—A comparison of ten species of *Ammophila* with respect to some aspects of the nesting behavior[3]

Species	Type of prey	No. of prey per cell	Nest depth in cm	Manner of carrying earth	Manner of carrying prey	Type of provisioning	Use of "tool"
procera	Notodontidae (r. Noctuidae) [Sphingidae]	One [? several]	7.2 (1.5-10)	Flies (r. walks)	Walks	Mass	No [Yes]
aberti	Geometridae (r. Hesperiidae)	Up to 10	7.1 (5-9)	Flies	Flies	Delayed [r. mass]	Yes
placida	Hesperiidae [Noctuidae, Geometridae]	3-5 [One]	6.7 (4-10)	Flies (r. walks)	Walks	Mass	No [Yes]
harti	Geometridae & looper-type Noctuidae	Up to 6	7.0 (3.5-10)	Flies	Flies	Progressive	No
juncea	Notodontidae & Noctuidae	1 or 2	4.8 (4-6)	Flies	Walks	Mass	Sometimes
urnaria	Noctuidae & Geometridae	1 or 2 (r. up to 6)	3.7 (2-5)	Walks (r. flies)	Walks (r. flies)	Mass (r. delayed)	Sometimes
aureonotata	Notodontidae [Hesperiidae]	One	5.0	?	Walks	Mass	No
nigricans	Noctuidae	One	[4.0]	?	Walks	Mass	?
xanthoptera	[Noctuidae]	[One]	[5.5 (2.8-6.5)]	[Walks]	[Walks]	[Mass]	[Yes]
pruinosa	[Micro-lepidoptera]	[Several]	[2.5-6.0]	[Flies]	[Flies]	[Mass, r. delayed]	[No]

3 Based mostly on my own observations. Data enclosed in brackets represent information taken from the literature; such information is cited only when it disagrees with my observations or pertains to species or aspects of behavior which I have not observed. The abbreviation r = rarely.

The most primitive wasps capture and sting a single host specimen, then usually conceal it in some manner, such as in a simple, unicellular nest in the ground, then lay their egg upon it and close up the nest. This sequence of behavior is exhibited by the genus *Podalonia,* which is closely related to *Ammophila,* and by other sphecine genera such as *Priononyx.* All species of *Ammophila* prepare the nest first, then close it temporarily while they undertake their hunting behavior. The stocking of the nest with a single caterpillar is unquestionably primitive; apparently *Ammophila aureonotata, A. nigricans,* and *A. xanthoptera* employ but a single caterpillar, and probably also *A. procera.* Hartman's report of more than one in the latter species in my opinion is questionable. This one caterpillar must, of course, approximate the wasp in size, and can scarcely be carried to the nest in any other way than over the ground. After the caterpillar is placed in the nest and the egg laid upon it, the nest is given its final closure.

It was an important evolutionary step when certain species acquired the ability to seek out a second caterpillar to add to the first. Some species (notably *urnaria* and *juncea*) appear to employ either one or two caterpillars, depending, one supposes, on the size of the caterpillars encountered in their hunting. Perceiving that the nest cell is not full, the female of these species (after oviposition) makes a temporary closure instead of a permanent one and then resumes her hunting activities. The amount of reorganization in the nervous system needed for this would, it seems to me, need to be rather slight. Yet this represents an important break-through in behavior. Once it had been accomplished, species could evolve which could exploit exclusively the smaller caterpillars in the environment. These small caterpillars could more efficiently be carried to the nest in flight. Such species as *aberti* and *placida* appear to represent this stage in behavioral evolution.

But such wasps, depending as they do upon the capture of up to ten caterpillars for a single nest, are sometimes faced with the possibility of being interrupted by darkness or inclement weather before provisioning is completed. I have observed, in *urnaria,* an actual case in which a female was interrupted by two full days of steady rain before she brought in her second and final caterpillar. In such cases, the egg may have hatched and the larva even be fairly large by the time the last caterpillar is brought in. "Delayed provisioning" of this type occurs not only in *urnaria,* but also in *aberti,* which uses up to ten caterpillars and exhibits it much more commonly. There may be some advantages (i.e., a certain amount of selective value) in such behavior; at least, the larva receives fresher caterpillars. True "progressive provisioning," in which the caterpillars are always brought in progressively as the larva grows, is apparently exhibited only by *harti* among the ten species considered. Such a species has a certain amount of "time on its hands" while awaiting the hatching of the egg and the growing of the larva; one species, at least, the European *pubescens,*

uses this time to prepare additional nests and begins provisioning one or two of them.

Thus there is a close relationship between the size and number of caterpillars used per nest, the way in which they are carried to the nest, and the type of provisioning employed. It will be noted from Table I that species which fly with their caterpillars also invariably fly with the earth which they dig from the nest; certain species, however, walk with their caterpillar and fly with the earth. To a human observer, the practice of flying from the nest with the earth from the burrow seems to be quicker and to result in a better scattering of the earth. Doubtless this behavior is advanced, since it occurs in relatively few other digger wasps and these rather specialized ones (e.g. *Anacrabro ocellatus*).

In general, the species of *Ammophila* do not appear to be very good lepidopterists, that is, they are not very selective of their caterpillars except as to size. Some species, such as *procera,* seem to hunt mostly in trees, where they take a preponderance of tree-dwelling forms, especially Notodontidae. Species such as *urnaria* and *harti* seem to hunt mostly in herbaceous vegetation, the latter species taking mostly if not entirely "loopers." Differences such as these, as well as the differences which can be noted in choice of nesting sites, doubtless function to lessen competition among the species.

The nests of all species of *Ammophila* are of simple structure and quite shallow. Differences in nest depth reflect, in part, differences in the size of the wasp. For example, *procera* and *urnaria* often nest in proximity, but *procera,* a much larger species, makes nests approximately twice as deep as *urnaria.* However, *harti,* a species no larger than *urnaria,* makes nests approximately as deep as *procera* and deeper than in the large species *aureonotata.* But *harti* nests in sand dunes, where there is danger of the cells becoming uncovered by wind action, and doubtless deeper nests are selected for. *Aureonotata* nests in hard soil and the nests are unusually shallow for so large a species.

Differences in position of the egg on the caterpillar, if any, are largely obscured by individual variation. This is a point worthy of further study, as other genera of wasps do exhibit differences in this aspect of the behavior.

There remains to be discussed the manner of nest closure. There appear to be four major components in this aspect of the behavior. (1) *Blocking* the burrow by placing one or more solid objects in the lumen, these objects being picked up from the ground around the nest and accepted or rejected, apparently, according to their size and consistency. (2) *Filling* the burrow by soil scraped in with the tarsal rake on the forelegs, augmented by lumps of earth or other solid objects added with the mandibles. (3) *Packing* the earth in the burrow (discussed further below). (4) *Concealing* the burrow by scraping earth in various directions over the top and often picking up various objects and placing them over the top. All species exhibit all four steps in

some form or other. They are best developed in the final closure of the nest, but the same elements appear during the temporary closure. Here, however, the blocking objects are placed near the top of the burrow and the other elements are correspondingly reduced. It should be mentioned that two species, *placida* and *xanthoptera,* which nest in rather firm soil, obtain most of the soil for filling by digging in one spot, making in fact a short "false burrow" near the true burrow. This behavior also occurs in the European species *campestris* and has been figured by Adriaanse (1947, Fig. 1).

The packing of the burrow (step 3) requires further discussion. Most of the packing is done with the oral surface of the head, with the mandibles spread widely; the body is held nearly vertically and moves up and down rapidly while the wasp emits a loud buzz. Packing with the head occurs in almost all members of the subfamily Sphecinae, but other digger wasps use the tip of the abdomen for this purpose. The term "pounding" is often used to describe these movements, but seems a bit too strong. The soil is actually pushed downward by the labrum, mandibles, and other mouthparts; a slight rotating of the head assists the up and down movements. As noted above, the filling is often augmented by lumps of earth or other objects picked up from the ground; these objects are selected after a much less elaborate behavior than that involved in blocking the burrow. Generally they are soft lumps of earth which are placed on top of the fill and then subjected to the same packing movements described above, which result in the lump being pulverized and spread out. Occasionally such lumps of earth actually remain in the mandibles during a few up-and-down movements before they are actually pulverized. Should the lump be hard, the wasp may merely force it down into the fill without breaking it. In some instances the hard object, often a small stone, may be held in the mandibles at some length during the packing process. At such times it doubtless functions to pack the soil further. Such objects are not always left in the burrow; after some pounding (the word is more applicable here) the pebble may be taken from the burrow and discarded. Presumably it is to the wasp's advantage that the burrow be packed as tightly as possible with fine-grained earth, and the leaving of pebbles in the burrow might provide undesirable air spaces.

It will be seen that there is a gradual progression from simple packing movements to the actual use of a pebble which is later discarded. At no point do we find evidence of the sudden flash of insight which the Peckhams thought they observed. Even the discarding of the pebble is not remarkable, for in other aspects of closure it is not uncommon for a wasp to remove from the burrow some object which it has just put there. This occurs during blocking, packing, and concealing, in each case the stimulus presumably being such as to indicate to the wasp that the object is somehow "undesirable." A progression such as this from simpler to more complex behavior may be termed an ethocline (Evans, 1957). Each step in this ethocline doubtless serves, in itself, some function of survival value to the wasp.

Some workers have been inclined to give the wasp credit for "using a tool" even if the "tool" is left in the burrow. In this case, however, it is difficult to be sure how much effective packing has occurred; all one can be sure of is that the object concerned has become part of the fill. If the pebble is actually discarded after use, then it has obviously functioned as a pounding instrument only. I suppose such a pebble will fit the dictionary definition of a "tool." Yet I hesitate to use the word in this instance, since to most persons the user of a tool is considered to have some perception of the result to be achieved, that is, to exhibit some measure of intelligence. It seems far more probable that the pounding behavior of *Ammophila* is nothing more than a particular combination of instinctive behavioral elements.

Why is it that some species apparently never "use a tool" (e.g., *harti*), others sometimes do and sometimes do not (e.g., *juncea, urnaria*), and others apparently always do (e.g., *aberti, xanthoptera*)? At this stage in our knowledge of the behavior of *Ammophila* it is impossible to answer this question. The necessary movements are probably available in all species, but it may be that a species such as *harti* lacks, in the innate mechanisms controlling the behavior of closure, the necessary nervous associations which would enable it to use a pebble for pounding. But it must be remembered that *harti* nests in sand dunes, where the soil consists of sand grains of more or less uniform size. It is difficult if not impossible to pack sand into a firm plug. *Ammophila harti* is a specialized species and may well have evolved from a form which nested in other situations where pounding with a pebble would have served a useful purpose; if one could force it to nest in firm soil, he might still be able to elicit this behavior. It is noteworthy that the species which "use a tool" regularly, such as *aberti* and *xanthoptera,* nest in rather firm soil. Species such as *urnaria* nest in rather diverse situations; in some cases the soil texture may be such as to elicit the full gamut of packing activities, while in other situations this may not be so.

Clearly this is a subject worthy of a great deal more study. Three lines of study suggest themselves as worthwhile. (1) More field data must be gathered on more species of the genus and on more individuals of the ten species considered here; these observations must be detailed and especially carefully made with respect to closing behavior. (2) An effort must be made to study one species in the field throughout its range and in all ecological situations in which it occurs. (3) An effort should be made to study one or more species under controlled conditions where he can manipulate such factors as soil texture, availability of various types of objects for filling, and the behavioral thresholds of the wasp.

In spite of shortcomings in our knowledge, two points seem clear. First, some species of *Ammophila* do pick up a pebble or some other solid object and pound the soil in the burrow with it, and some species do it with great regularity. At least 16 observers have seen this be-

havior in at least 9 different species (6 North American and 3 European).[4] Second, interesting though this behavior is, there is nothing about it to justify the publicity it has received. *Ammophila* is very far from being "comparable to the man or ape who first took a stone in his hand to crack a nut" (McDougall, 1923). It has merely found a functional value in combining two or three very simple innate acts in a new way.

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[4] The European species are *heydeni, sabulosa,* and *campestris*. For references and discussion, see Baerends (1941, p. 94) and Thorpe (1956, pp. 248-249). Both these authors, incidentally, come to conclusions very similar to mine. Thorpe says: "those species and individuals which use a pebble as a hammer . . . appear merely to be combining two features of the instinctive hole-filling process in a rather unusual way." But he adds: "since the animal is constantly manipulating clods and stones, it has every opportunity to learn by trial and error, from the chances of its normal experience, the results of handling hard objects of various kinds."

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Population Control in Guppies

S. MERYL ROSE
University of Illinois, Urbana

Populations of aquatic organisms appear to be self-limiting (Rose, 1957, 1959, 1960). Breder and Coates (1932) have shown for the guppy, *Lebistes reticulatus,* that 5.5-liter aquaria would support 9 adult fish. This was their final number whether they started with one or 50. Once nine had become adult, even though more were born, no more could survive to adulthood. Apparently young guppies grew up only as replacements for older ones that died. Shoemaker (1944) repeating the observations found that a steady state is reached but that in time the numbers drop off from the plateau. After two years a new cycle of population growth began.

Breder and Coates believed, but did not demonstrate, that population was controlled only by infanticide. The data presented in the present paper indicate that both the production and survival of guppies decrease as numbers of adults increase.

Experiments

Preliminary observations indicated that the number of young produced per guppy varied inversely with the number of adults present. Single females in 12-liter aquaria have been observed to produce as many as 60 young at a time. Females in groups of 10 seemed to have appreciably fewer offspring.

Two questions were asked. Does the number of young obtained per guppy actually decrease as more adults are kept together? If so, is this a species specific effect? In other words, do other fish living with guppies affect the production of guppies? To answer these questions aquaria were set up containing different numbers of guppies. In addition some of the aquaria also contained White Cloud Mountain fish, *Tanichthys albonubes.*

The experiments were conducted in aquaria containing 12 liters of water. The aquaria were planted with *Anacharis, Fontinalis* and *Hygrophila,* and snails of the genera *Physa* and *Helisoma* were added. Approximately one-third of the water was replaced once a week by tap water which had stood for one day. Forty-watt bulbs at a distance of 10 cm from the aquaria were kept lighted from 8 to 12 hours per day.

Different numbers of newborn guppies were added to 10 aquaria: 3 were stocked with 14 guppies each; 3 with 10; 3 with 2 and 1 with 1 guppy. Before young were produced, one guppy had died in each of three aquaria, reducing their numbers to 13, 9 and 1 (Table I). The fish were fed as much as they would eat four times daily. The

TABLE I.—Numbers of adults of two species related to the number of young produced by one of the species during three months

	1	2	3	4	5	6	7	8	9	10
Number of Adult Guppies	14 6♀, 8♂	14 6♀, 8♂	13 5♀, 8♂	10 6♀, 4♂	10 5♀, 5♂	9 5♀, 4♂	2 1♀, 1♂	2 1♀, 1♂	2 1♀, 1♂	1 1♀
Number of White Clouds	0	3	0	6	0	0	12	0	0	0
Numbers of Young Guppies Recovered in a Single Day	4 1 4 2 1 2 6	4 6 5 12 5 12 23 16 15 6	2 2 7 8 6 7 8 5 21 5 14	18 51 4 2 4 40 29 8	14 3 1 6 6	21 6 26 17	7 12 5 26	5 29 23	4 13 34	8 46 46
Totals	20	104	85	156	30	70	50	57	51	100
Average Number of Young Obtained per Guppy	1.4	7	7	16	3	8	25	28	26	100

foods were dried brewers' yeast, fresh liver, yolk of hard boiled egg, *Enchytrea,* and Purina Rabbit Chow. The latter, a relatively non-fouling food, was usually present in slight excess so that some food was always available. Excess was siphoned from the aquaria every few days.

After the fish had begun to produce young the aquaria were examined at least twice daily for newborn fish. All were removed and counted and not returned to the aquaria. The numbers in Table I indicate the numbers of young found in a single day.

The experiments indicate that the number of young obtained per adult is inversely proportional to the number of adults. This can be seen from the numbers across the bottom of Table I. When 13 and 14 guppies were present without white clouds the numbers of young obtained in the first 3 months of production ranged from just over 1 to 7 per guppy. The range for 9 and 10 adults without white clouds was 3 to 8. Approximately 26 young were obtained per adult when one pair of adults was kept in an aquarium. The number jumped to 100 when a female remained isolated in an aquarium. Her mate had died before the first batch of young appeared, but sperm are retained by females for several months.

The 100 produced by this lone female was more than the total produced by 5 or 6 females in the groups of 10-14 fish. The only exceptions where a group of females outproduced the isolated female were in the aquaria where, in addition to guppies, there were white clouds. The lone female produced many more than any of the females in groups. Her closest competitors were the females of single pairs and they averaged only one-half as many per female.

It is quite clear that as more guppies live in an aquarium fewer offspring can be obtained from each. This is in the presence of as much food as the fish will take. The mechanism limiting production cannot be a scarcity of food.

In addition to guppies, three of the aquaria contained white clouds (see Table I, line 2). The white clouds are smaller than female guppies, but larger than males. An average pair of white clouds weighs almost as much as an average pair of guppies in which the female is not pregnant. The question was whether white clouds would substitute for guppies in limiting the number of young obtained. The experimental design was such that all aquaria containing white clouds had approximately the same amount of fish (guppies plus white clouds).

Column 7 in Table I indicates the numbers of guppies obtained when in addition to a pair of guppies 12 white clouds were present. If the white clouds were acting like guppies in limiting young guppies, and if they were as effective per unit weight as guppies, there would have been the equivalent of almost 14 guppies.

Fourteen guppies alone had produced less than 1.5 young per adult (column 1). Thirteen had produced 7 per adult (column 3). Ten and 9 had produced 3 and 8 (columns 5 and 6). This group

of 2 guppies and 12 white clouds had a production per guppy very unlike that for the above large groups, but almost the same production as the pairs without white clouds. The pair with white clouds produced 25 per adult whereas pairs alone produced 26 and 28 per adult. The difference between 25 and 26 or 28 is not significant. There is no effect of white clouds on the production of a pair of guppies comparable to the marked inhibitory effect of the presence of other guppies.

The number of young guppies obtained in the 9 and 10 guppy series was unusually high when 6 white clouds were present (column 4). It is quite clear that the addition of white clouds to 9 or 10 guppies had not further limited the production of guppies. More experiments would have to be done to determine whether the apparent stimulation of guppy production by white clouds in this number range is real. There may be another reason for this result and it is considered below.

In a third group where white clouds were kept with guppies the number of young obtained from the guppies was not reduced by the presence of white clouds. This can be seen from a comparison of columns 1-3.

When the data are regrouped as in Table II, one can see that from 50 guppies, 313 young were obtained. Approximately half as many guppies, 26, but with white clouds, yielded 310 young. Those with white clouds produced almost as many but in only half the number of aquaria. If the averages per aquarium or per volume of water are considered, guppies alone yielded at half the rate of guppies with white clouds. This is true when the above totals are considered but was not true in all size groups. When the largest groups are compared, 14 guppies with white clouds yielded 104 babies while the average for 13 and 14 guppies alone was only 53. Similarly, 10 adults with white clouds yielded 156 and the average for 9 and 10 without white clouds was only one-third as many young, 50.

TABLE II

Number of Adult Guppies	Baby Guppies		Number of Adult Guppies	Number of White Clouds	Number of Baby Guppies
	Number	Average			
14	20		14	3	104
		53			
13	85				
10	30		10	6	156
		50			
9	70				
2	57		2	12	50
		54			
2	51				
50	313	157	26	21	310

Only for the single pairs are the numbers of young obtained from guppies with and without white clouds approximately the same, 50 for the pair with white clouds and 54 for the pairs without white clouds.

Possibly the number of offspring actually produced was not different in the groups with and without white clouds, but only became different as crowded guppies without white clouds ate more of their own young.

It is also possible that the production was actually greater in the larger groups when white clouds were present. Unfortunately none of these females was isolated before giving birth and thus the actual number produced was not determined.

Although it is not clear whether those in the larger groups with white clouds produced more or ate fewer or both, it was observed that members of larger groups without white clouds as contrasted with pairs, or with the isolated female, produced fewer and ate more. Both methods of limiting young were observed. In Aquarium 1 with 14 adults and in Aquarium 5 with 10 adults some individuals were observed chasing, catching and eating young. On the other hand it is doubtful if members of pairs or the single female, under the conditions of this experiment, ever chased and captured their young. Many hours were spent in observation, but no persistent chasing of young by the pairs or the lone guppy was seen.

Differences in girth and behavior were obvious when pregnant females from larger and smaller groups were compared. The lone female and the females of single pairs attained much greater girth in late pregnancy than did females in the larger groups. A few females were isolated just before giving birth, their number of young counted and their behavior observed. Three females from the larger groups were placed singly in large unplanted jars and watched. They bore 2, 3 and 8 young. The one which bore 3, chased and ate all 3 a short time after birth. Those which bore 2 and 8 were removed from their young an hour after the last young had been born and had not eaten any in that time. The single female of Aquarium 10 was also removed to an observation jar where she gave birth to 46, did not chase any and had not eaten any in 24 hours, after which she was returned to her aquarium.

As in other cases of population and growth control in aquatic organisms (Richards, 1958; Rose, 1957, 1959, 1960) a water borne factor appears to be involved. A preliminary experiment indicating that this may be true for guppies has been performed. Eleven recently matured females and one male were kept in a 14-liter aquarium with approximately one-fifth of the water changed weekly for a five-month period. They were fed maximally. During the five months none of the females increased in girth appreciably, and no young were seen. If any were born, they were very few and were promptly eaten. At the end of the 5 months one-third of the water was exchanged two or three times daily with aquaria containing other

tropical fish but no guppies. After 25 days of water exchange five babies appeared, and two more appeared two days later. The babies swam directly over and between the adults without being molested. Apparently whatever controls the production of guppy babies and puts them in the food category for adults is a guppy factor and can be diminished by replacing large amounts of the water in which they live.

DISCUSSION

Many organisms are known to add something to their culture water which decreases growth and reproduction. These are as diverse as bacteria, echinoderm larvae, *Daphnia* and frog tadpoles. Likewise higher plants are known to add substances to their soil which limit their growth. This has been demonstrated for peach trees (Proebsting and Gilmore, 1941) and for cereal grains (Schönbeck, 1956).

Wherever studied the substances have been rather specific, acting back on the growth of the same and closely related species, but not on members of different families. For example, culture water in which a single species of sea urchin had grown prevented growth of young larvae of the same species, greatly inhibited growth of larvae of a closely related species, but was better than fresh sea water as a culture medium for more distantly related echinoderm larvae (Vernon, 1899).

In the present experiment there is evidence that while guppies are self-limiting white clouds do not limit guppies, providing of course that other factors such as oxygen and food are adequate. White clouds, although not limiting guppies, do add to their water very effective substances limiting their own populations (Rose, 1959).

Another generalization that can be made regarding population control is that larger growing members of a population inhibit the growth of smaller members. This was clearly demonstrated for trout by Margaret Brown (1946). Trout fry were kept in groups under conditions favoring growth. In a few months time there was a great range in size in all groups. The larger were growing rapidly and the smaller grew much less rapidly. Some died and it was always the smallest that died. This happened in the presence of as much food as the fry would take and there was no evidence of attacks on the smaller fish.

When fry from two aquaria were regrouped so that the smaller of both shared a new aquarium and the larger of both groups also shared new quarters, individual growth rates changed. The largest of the newly formed group of smaller fish began to grow much more rapidly and in a few months approached the size of the largest in the group of larger fish. In the other aquarium the smaller of the newly grouped larger fish grew more slowly than before and at the end of the experiment were smaller than many of those which in the original groups had been smaller than they. It seems to be a

general rule that something from larger growing members of a species may inhibit the growth of smaller members of the same species. This has been demonstrated recently for two other fish, *Tanichthys albonubes* and *Barbus tetrazona* (Rose, 1959) and for anuran tadpoles (Rose, 1960).

This brings us to a consideration of what factor or factors may induce more concentrated guppies to eat their young. We tend to think, and it is the popular conception, that crowded guppies are so hungry that they eat their young. However, as many have learned, no amount of feeding will prevent cannabalism by crowded guppies, or by uncrowded ones, whose water is not changed. Possibly the initial change effected by water borne products is in the young. If the general rule operates here, the water borne specific products should affect the young appreciably more than their larger parents. The affected individuals may as a result exhibit a behavior to their elders that leads to their elimination.

The cue, if there is a cue, which promotes the attack on young by adults is not known. One observes in crowded and uncrowded aquaria that adults approach newly born young. This behavior seems to be a test for the young. If the young dart off on the approach of an adult they are not followed relentlessly. This is certainly true in the uncrowded, well-planted aquaria. In crowded aquaria adults, often in groups, seem to seek out the young, chase relentlessly and capture them. Possibly the initial cue for attack by the adults is a slower rate of response and motion by the young when guppy products are in high concentration when the young appear. As far as I know there have been no experiments to test whether the initial effect leading to elimination of the young in crowded quarters is a change in the young or a change in the adults.

The addition of unrelated species, even though this increases the need for food and oxygen, increases the survival of young guppies. It is not known how this is accomplished, but it is often found that unrelated species are mutually beneficial. For example, tadpoles grow appreciably faster when other, not closely related animals such as snails and salamanders are kept with them (Rose, 1960). The suggestion has been made that the species or genus specific inhibitors may in part be metabolized away by relatively unrelated members of a community.

SUMMARY

The production of guppies varies inversely with the concentration of adults.

The number of young eaten increases with density of the adult population.

Under crowded conditions more young guppies survive when white clouds are grown with them. Under uncrowded conditions no effect of the white clouds could be observed.

The fact that water changes with conditioned water from other

kinds of fish increases guppy production and partially eliminates the effects of crowding leads to the suggestion that guppies may belong to the growing list of organisms for which it is known that rather specific water-borne products act to limit the population.

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The Occurrence of Marine Actinomycetes in Texas Gulf Coast Substrates[1]

A. W. ROACH and J. K. G. SILVEY
North Texas State College, Denton

The aquatic actinomycetes as a discrete habitat group, comprise a group that has been more or less neglected; a greater proportion of actinomycologic research has been concentrated on the soil and pathogenic forms. This is a natural development as the latter are important as pathogens and producers of antibiotics. However, in 1950 Silvey *et al.* correlated noxious tastes and odors in surface water supplies with the by-products of fresh water (glykophilic) actinomycetes. Thus the aquatic forms became economically important and worthy of extensive study. Previously, algae had been considered to be the offending organisms even though no algal by-products had been isolated and diluted in odor-free water to duplicate the unpalatable musty, woody, earthy or hay-like tastes in municipal waters.

The resultant series of studies on the fresh water forms eventually created an interest in the marine strains. The fresh water studies stressed the odor and taste production problem, control, and limnology with notes on taxonomic, morphologic, and cultural characteristics (Silvey and Roach, 1953; 1956). In 1958, Roach and Silvey reported on the morphology and life cycle of a number of fresh water isolates and found that many produced both lateral and chain spores on the same secondary hyphae. This observation was of interest since those actinomycetes that produce lateral spores are placed in *Micromonospora* and those that produce chain spores, in *Streptomyces*.

In 1956, a halophytic actinomycete was obtained from a sample of *Cladophora* from an intertidal pool with a salinity of 35 ppt from Bray's Island, North Carolina. This isolation, together with another from macerated *Sargassum* taken from the Gulf of Mexico near Galveston, Texas, plus the fact that actinomycetic odors are commonly observed in the estuaries or the lagoons of the Gulf, indicated that the marine habitats should be investigated. There was always the possibility that the activities of the marine actinomycetes would not be too different from those of the forms which had been isolated from soil, fresh water, and composts. The work was commenced in 1957 with the viewpoint of sampling the Texas Gulf Coast, concentrating on isolation and then investigating the morphology, degradatory activities, odor production and pathogenicity of the resultant isolates.

In 1957, a literature on the marine actinomycetes was sparse. There were isolated reports, mostly from general studies of marine

1 This research was supported by NIH Grant-in-aid E-1519.

microorganisms, such as that of Rubentschik (1928) who isolated cellulose-decomposing organisms from the bottom deposits of the Black Sea, one of which was an actinomycete. The one major reference to marine actinomycetes *per se* was that of ZoBell *et al.* (1943). They reported that the majority of the hydro-carbon oxidizing marine microorganisms were from *Proactinomyces* (mostly *Nocardia*), *Actinomyces* (*Streptomyces*), *Micromonospora, Pseudomonas,* or *Mycobacterium.* They further stated that 5-10 percent of these microorganisms were species of *Proactinomyces* (*Nocardia*); whereas, very few *Actinomyces* (*Streptomyces*) were found in stations remote from terrigenous contamination.

In November, 1958, Grein and Meyers reported a series of studies initiated simultaneously in 1957 at Rutger's Institute of Microbiology and the University of Miami Marine Laboratory. They secured 87 isolates from 85 samples taken in Florida; 172 isolates from 8 samples taken in New Jersey; 3 isolates from one sample from the Bahamas; and no isolates from two samples from the Gulf of St. Lawrence. They secured superior isolation on a starch-casein agar and particularly an increase in the number of colonies when distilled water was substituted for sea water in the medium.

When these isolates were compared with terrigenous types on the basis of soluble pigments and the color of vegetative and aerial mycelium, they found that one-fifth of their isolates were *Nocardia* and *Micromonospora.* The remainder of the isolates were *Streptomyces* which they placed into eight general groups. On this macroscopic basis they found no apparent morphological differences between their sea isolates and the terrestrial-type species.

The remainder of their paper was concerned with a basic and first question: namely, are the marine actinomycetes a specifically adapted habitat group or are they halotolerant terrigenous forms? They believed the latter was probably true since their results indicated such a wide variety of response. Their postulation was based on the fact that there was no apparent morphological difference between the marine and terrestrial isolates and the fact that many of the terrestrial actinomycetes showed a wide salinity tolerance, with good growth on 100 percent sea water nutrient media. Although these authors felt that their initial studies were inconclusive, they are a major step in the recognition of this neglected group.

The purpose of this paper is to report on isolation and salinity response with a description of the diversity of microbiological habitat of the rather unique Texac Gulf Coast, and to examine the types of substrate from which the actinomycetes were collected in order to form a possible basis for correlation of the results obtained under artificial laboratory conditions in the subsequent morphology, degradatory, odor production and pathogenicity studies. Taxonomic considerations and correlations will be reserved until the evidence from all studies is obtained.

THE TEXAS GULF COAST

The Texas Gulf Coast as a littoral province differs markedly in its combined physical characteristics from other coasts of the United States. In turn the specific resultant environmental complex or holocoenosis affects the relative potential of biological productivity. This relationship might best be deciphered in part by examining each of the physical characteristics.

First, the continental headland is of soft Cretaceous ocean beds which have been easily pulverized over the past sixty million years into fine sand. The action of transilatory waves on this type of substrate has created a typically shallow eulittoral and sublittoral profile, which drops off approximately one fathom per mile within the offshore zone. In addition and because of the shallow benthos, two ridges have been developed. The first ridge is benthic and parallel to the coast in the sublittoral terrace. This is typical of wave action against a shallow sandy shoreface.

The second ridge is an extensive system of barrier bars or islands parallel to the coast (Fig. 1). According to A. L. Kornicker, University of Texas Marine Institute (personal communication), the most probable explanation for such an extensive development along the Texas Coast has been the past periodicity of hurricane tides expelling their force radially into the Texas basin. These large storm waves expend their energy on the bottom of the shelving shore further out than do smaller waves. The bottom is deepened and coarse particles move landward to form a bar enclosing a lagoon (Johnson, 1919).

The extensive shallow lagoon system resulting from the barrier island development was of particular interest in this study. These lagoons or bays, as they are usually called, are shallow sediment and debris traps. Continental sewage, industrial waste and stream debris tend to concentrate behind them. Marine debris may be driven through the "passes" or over the island bars in some areas during seasonal storms. Likewise, the still, shallow waters of the lagoons are conducive to sedge-grass swamp development. This is of particular importance again because of the nature of the headland substrate. In the eulittoral zone on the surf side of the island, the shifting sands offer no purchase for marine algae. Thus, the biological productivity such as one finds in tidal areas along rocky headlands is reduced to a comparatively low point because of the resultant absence of benthic communities. Some pelagic material is washed up on shore seasonally and adds enrichment to the intertidal habitat. Away from shore, plankton samples of a mile may at times yield very little material and an evident biocycle of any kind is found only under floating logs. Such relative sterility increases the importance of the barrier island and the resultant lagoons or bays behind them.

Another important factor complex is that of coastal fresh water influent. In turn this is controlled by the Rocky Mountain chain

which constitutes a barrier against the prevailing northwesterlies. The resultant rainshadow precludes arid conditions and one would expect hypersaline bays where there is a limited exchange across the barriers. In Texas, this is modified on the coast from Corpus Christi eastward by the Gulf Tropical Air Mass. The northwesterlies as a specific Polar Pacific Maritime Air Mass enter the United States in the Washington and Oregon area crossing the continent and leaving in the area of Maine. The Gulf Tropical Air Mass is pulled up from the Gulf into the suction created by the pulses of this northwesterly movement. As a result, the rainshadow effect does not extend very far from the barrier and there is an increasing gradient of precipitation eastward from it. In general, this amelioration creates in the bays

Fig. 1.—The Texas Gulf Coast. Note the extensive barrier bar development and the enclosed lagoons. The letters signify the sampling areas.

west and south of Corpus Christi a salinity greater than 35 ppt and in those north and east a salinity lower than 35 ppt.

The over-all pattern varies cyclically since during some years a greater percentage of the northwesterly storm tracks are approximately straight across the continent whereas in other years most of the pulses dip sharply to the south in the midcentral states. In the former case, the rainshadow effect is extended to the east and salinity rises in the bays eastwardly. In the latter case, the rainshadow effect is lessened and the salinities become very low to the east and drop below 35 ppt in the southwestern bays.

During the diurnal intertidal exchange there is very little mixing between the Gulf and lagoon waters through the limited number of passes. The mixing that does occur is probably during the equinoxial tides. Thus, in the normal exchange during one year one would expect bay salinities to be high in the spring, becoming brackish from the vernal run-off, particularly near the river effluents and continuing through the summer, except where evaporation would raise the salinity in cut-off arms, until the autumnal exchange between the Gulf and the bays.

Specific hydrographic work has been done on the littoral waters of the Texas Coast in selected areas. Collier and Hedgpeth (1950) made salinity and temperate determinations at scattered stations centered around Aransas and Copano Bays. A few determinations were also made in Baffin Bay, Corpus Christi Bay, and the Gulf at Galveston. Like data collected last year in the course of this project are given for the comparable areas in Table I. In general the data show that the lagoons south of Corpus Christi have salinities varying from 80 ppt throughout the year in the drier years dropping as low as 4-10 ppt in the wetter years. The Gulf waters as shown by the Galveston determinations are fairly consistent in that they range from 20-32 ppt regardless of the amount of fresh water that is introduced into the bays. In making comparisons of these data it should be noted that the precipitation over the Texas watersheds as a whole was 150 percent higher during the past year than during the late 1940's when the Collier and Hedgpeth data were collected. This point is evident in the difference of the yearly ranges of Aransas Bay, which is typical

TABLE I.—Comparative salinities (ppt) of four Texas coastal areas. C-H salinities are those reported by Collier & Hedgpeth (1950) and R are those which we recorded this year for the same areas. The areas are: GG—Galveston Gulf; AB—Aransas Bay; CCB—Corpus Christi Bay; and BB—Baffin Bay (*vide* Figure 1 for location).

	Salinities			
Invest.	GG	AB	CCB	BB
C-H	20-30	19-20	10-26	40-80
R	23-32	1-15	16-25	70

of the hyposaline bays. The range dropped to 1-15 ppt during the wetter years from 19-20 ppt.

Breuer (1957) studied ten stations on the northern end of the Laguna Madre below Corpus Christi, September, 1951 to March, 1953. He found the average mean salinity was 52 ppt with a high of 75 ppt and a low of 1.4 ppt. The low occurred following a heavy rain at Loyola Beach. He also reported on the effects of the Texas Fish and Game Commission to open and keep open a number of passes through Padre Island in order to lower the salinities to improve the productivity of the lagoons for fishing. Salinity determinations proved that there was little or no mixing effected; salinities dropped less than 1 percent, only within one-half mile of the passes.

SAMPLING STATIONS

In order to facilitate sampling, the coast was first divided into arbitrary sections which were lettered in order to simplify sample coding (Fig. 1). The demarcation of the areas was largely determined by the availability of the roads leading into potential stations and by the physical characteristics of the coast line. Stations and samples were numbered consecutively. Each sampling series was recorded on separate station sheets as to sample numbers, substrate of each sample, date, salinity, and temperature, together with pertinent notes. Samples were taken of the water, mud, algae, and plant and animal remains.

GULF BEACH INTERTIDAL STATIONS

The gulf beach-intertidal stations were almost identical with the exception of the Sabine headland, a ten-mile strip near the Louisiana border. The substrate is fine, uniform sand with a shallow, flat beach merging into well-developed dunes. During the summer the intertidal zone is relatively sterile and the samples taken were of the water and sand and the washed-up vegetation and debris that could be found. During the spring there are large windrows of *Sargassum* and string coral washed up at the high tide mark (Fig. 2.5). During the fall much of the debris is plant material which has washed down Central American rivers. Periodically throughout the year there may be considerable quantities of jellyfish and other animal remains deposited. Samples of all of these materials both wet and dry were collected. Locations of these stations were at Port Isabel, Mustang Island, Matagorda Island, Surfside, Texas, the J area, Galveston Island, and the extensive shell beaches in the E area, fifteen miles southwest of Sabine Pass, Texas.

In the Sabine area there were two gulf intertidal stations which differed somewhat from the preceding. Fifteen miles southwest from Sabine Pass the coast is sandy with considerable shell deposits of shallow depth merging into the coastal prairie. There is little or no dune

Fig. 2.—Selected Texas Gulf Coast sampling stations: 1—Sabine headland gulf beach; note the washed-up debris from the Gulf and nearby coastal salt marsh and the lack of dune development; 2—Galveston Bay at Texas City near a chemical plant; black wastes are suspended in the water and coat the substrates; 3—Sabine salt marsh headland at low tide; note the rich mud and algae on the channel retaining wall and swamp in background; 4—Aransas Bay shallows; note the oyster reefs and sedge islands in background (this is typical of the barrier island lagoon which represents the best possible habitat enrichment since it traps vegetation and human waste and the substrate does not constantly shift as it does in the Gulf eulittoral); 5—*Sargassum* washed up at high tide on Mustang Island; such material represents the best source of

development. Some of the material that is washed up is apparently from the coastal swamps to the east and is mixed with the usual materials found on the intertidal zones of the other stations (Fig. 2.1). On the Sabine headland the eulittoral is a dense swamp composed principally of *Spartina patens* (L.) Kunth. This particular station was located at the Sabine Pilot Station which had a low cement retaining wall to keep back the mud (Fig. 2.3). Samples taken were of the *Cladophora* growing on the wall, of the rich mud, water and decayed grass sheaths.

Salinities at the Sabine Pilot Station range from 19 ppt in the spring to 22 ppt in the fall. This range was lower than that of the other Gulf surf stations and was probably due to the proximity of the Sabine River. The next lowest range recorded was that of the Sabine Beach station fifteen miles west from Sabine Pass which had a range of 22-26 ppt. The remaining gulf beach intertidal stations had a range of 30-32 ppt.

In the E area, two stations were located along the pass between the Gulf and Lake Sabine. The station near Sabine, Texas, was composed of a shell, mud and swamp grass margin (salinity 9-31 ppt). The station along the ship channel at Sabine Pass, Texas, had an oyster shell margin with attached algae and some evidence of industrial pollution from the large refineries at Port Arthur (salinity 4-11 ppt).

The stations in the A and B areas of the thirty-two remaining stations behind the barrier bars were the least polluted of the hyposaline sites. The samples were of uncontaminated substrate except where specific efforts were made to collect around bait stands and the beach areas of the villages. These areas have become established mainly as fishing and retirement centers; whereas, one finds heavy industry and population in the Galveston, Corpus Christi, and Freeport areas. The least disturbed and also most inaccessible were the G and H areas. This is due undoubtedly to the infertility of the hypersaline Laguna Madre.

Two stations (A2, A3) were located along the causeway which transects Aransas Bay from Aransas Pass to Port Aransas. In this area the bay is extremely shallow spreading out into broad, barren flats of fine sand quite often with oyster and sedge bars; the sand overlies layers of decaying sea vegetation (Fig. 2.4). The water is usually clear but contains a tan floc around the margins. The diurnal temperature range is broad due to the shallowness of the water and our determinations show that the seasonal variation is at a high level. In January the water is around 20° C to as high as 40° C in August. Salinities, in the determinations made so far, range around 27 ppt.

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microflora since the eulittoral is barren; 6—Sedge and grass islands in Aransas Bay; 7—Oslo Bay, an arm of Corpus Christi Bay, filled with sewage sludge; 8—Galveston Bay at Galveston, typical of human pollution.

Samples were taken of the sand, floc and sediment on the oyster shells, sedge bases, water, and the reduced and fresh wet or dried marine vegetation.

The variation of eight station types in the northern part of Aransas Bay, St. Charles Bay and Copana Bay was of mud coatings on riprap and *Cladophora* mats at the strait between Aransas and Copana Bays. Sedge flats of rich mud with heavy actinomycetic odors were along the bay above Fulton (salinity 5-11 ppt) (Fig. 2.6). A small cut-off lagoon was built by extra high tides through a conduit. It had a very shallow mud bottom and *Distichlis* margin and a salinity range somewhat higher than that of Aransas Bay because of evaporation in the summer. St. Charles Bay was a spoil basin and because of its position receives large amounts of marine vegetation which may persist as mats along the lagoon margin for months. Its bottom consisted of fine sand and oyster shell and small islands of sedge and various swamp grasses. At this station, samples taken of the decomposed vegetation and the mud floc on the various substrates around a fish-cleaning station were rich in complex proteins (temperatures ranged from 21° C in the winter to *ca.* 35° C in the summer; salinities that were checked ran very low, principally around 6 ppt.

The C, D, J, and F hyposaline stations were adjacent to areas of large population or industrial installations. At Galveston five stations represented the following types: (1) West Bay receiving no major continental drainage and open to the Gulf to the west by a narrow strait into Galveston Bay; the substrate is principally of oyster shell with some fine sand and with a usually restricted marginal sedge development; at one station samples were taken around a very polluted bait stand area of sand, mud, water, and shell scrapings; toward the east end of West Bay along the Galveston shore line the water is ladened with suspended material and the margin polluted with refuse (Fig. 2.8); salinities extended from 13-22 ppt with a temperature range of 25-35° C throughout the year; (2) clay and sedge flats on Galveston Bay proper along the continental shore line which receives considerable pollution from the city; samples were of the turbid mud, sedge bases, clay substrate and washed-up debris; salinities were a little lower than in West Bay and ranged from 11 to as high as 19 ppt in the fall; (3) chemical pollution at Texas City; the water black due to a suspended load of floc, the fine sand and sedge vegetation black with chemical waste coatings (Fig. 2.2); samples were of the floc, black sand and vegetational bases; salinities were from 10 to as high as 18 ppt; (4) East Bay has the same physical characteristics as West Bay except there is less pollution and a greater sedge development.

In the J area two stations were set up in the old Brazos channel and in the newly dredged Brazos River channel, both being used by industry as ship and waste channels. The channels have mud bottoms with grass growing down to the high tide level. The water was highly polluted and samples were of the mud and water. Salinities ranged around 5-6 ppt in the new Brazos River channel due to the dilution

of the Brazos River; whereas, they were around 20-26 ppt in the old channel.

In the Matagorda area, one station was established on the Matagorda River just beyond the surf and near a bait stand. The salinity was from 3-5 ppt due to the dilution of the river but highly polluted. At Palacios a shallow arm of Matagorda Bay with some shell, a mud bottom, small patches of sedge at the margin, and turbid water yielded our greatest number of isolations. The salinity extended from 16-18 ppt. At Point Comfort of Matagorda Bay samples were taken from an extensive clay bottom flat adjacent to a large industrial plant which was heavily polluted from a nearby bait stand. Salinities were fairly constant throughout the year at *ca.* 10 ppt.

Observations of the waters and the odors of Corpus Christi Bay leave one with the impression that it is little more than a large sewage lagoon. The stations located on the causeway transecting the bay from Mustang Island to the headland were much the same as those across Aransas Bay as far as physical characteristics were concerned. The water was much more turbid carrying a heavy load of suspended material and much higher in nitrogenous content than at stations further north. Stations were located that corresponded closely to those of the A and B areas. As Corpus Christi dumps a fairly large amount of sewage directly into Oslo Bay, samples of saline sludge were obtained (Fig. 2.7). At one station along North Beach of Corpus Christi Bay samples were taken behind a tourist court and bait area where an open sewer emptied into the bay. Salinities ranged from 16-25 ppt.

A road leading to the Laguna Madre was located out of Riviera Beach on Baffin Bay. The hypersaline waters contained little or no vegetational material. The substrate was clay. Further south at Port Isabel there were several types of natural and polluted areas along the causeway and on the Padre Island side of the Laguna Madre. The waters in general were a little deeper and there was a noticeable absence of sedge flat development in the bay as found further north.

SUBSTRATE AND SALINITY RELATIONSHIPS OF THE ISOLATES

It is often difficult to obtain high yields of discrete actinomycetic colonies from aquatic substrates. Even though there may be some indication of the presence of actinomycetes in the sample such as odor or mycelia and spores, failure to isolate them on enriched agar is not uncommon. Because of this difficulty many different methods were improvised based on differential responses of the competing microbial populations to unfavorable environmental conditions such as desiccation, application of inhibitors to the diluted sample, and differential use of carbon sources in order to free the less aggressive actinomycetes.

The technique which might be designated as differential desiccation is based upon an observation that the greater part of the bacterial

flora in diluted sample will rapidly increase on an isolation plate and die out as the agar dries out. The actinomycetic colonies usually appear and grow following this bacterial succession. One might interpret this phenomenon as an inhibition and competitive release mechanism with the actinomycetes having a wider amplitude to grow in lower water tensions.

Approximately a gram of each of the 612 samples collected was diluted at least 1:100 with 100 ml of filtered sea water and plated onto approximately 1,350 "desiccation plates." The procedure consisted of pipetting 1 ml of the dilution onto the plate just as the 3 or 4 percent agar hardened at a temperature of approximately 47° C. At first it was believed that this would augment the dehydration of the more susceptible bacteria or at least destroy a large number of them immediately, since the 3-5 percent agar would take up the excess water and leave the diaspores of the organisms on the surface of the plate. The plates were incubated at room temperature and checked daily for one to two months. The actinomycetic colonies that appeared were usually depauperate but when freed, so to speak, usually grew rapidly and produced a colonial mass on the transfer plate. Emerson's medium was used in this isolation series.

By the end of 1957, the isolate yield appeared to be lower than it should be. It seemed probably that a fraction of the actinomycete

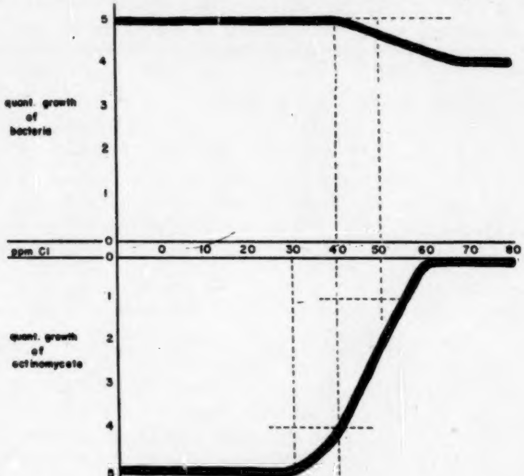

Fig. 3.—Response of selected marine actinomycetes and bacteria to varying concentrations of Cl. Differences in response are based on a 5-point qualitative scale. Note that the reverse desired effect is obtained as far as isolation procedure is concerned in that bacterial competition is not reduced but favored.

population in the sample had the adaptive capacity to withstand dehydration and that the inhibited remainder was being lost along with the bacteria.

Yield increase was sought by differential treatments of the competing floras primarily in the dilution flasks. First, it was hoped that the bacteria could be differently screened by passing the diluted sample through a Millipore filter since most actinomycetic spores range from 0.6-0.8 μ in diameter, or were smaller than most of the bacteria encountered. In test runs, spore suspensions of pure isolates were passed through Millipore filters with an 0.8 μ porosity. When the filtrate was enriched the results were negative. The technique was abandoned when various washing compounds failed to unclog the pores.

Next, the selected bacteriastatic effect of copper and chlorine was investigated. Dilutions of spore suspensions of purified actinomycete isolates and of a large series of selected samples were treated with various concentrations of copper and chloride for different lengths of time. At the end of each time interval, 1 ml of each treatment was plated on Emerson's medium. The results of these treatments are shown in Figures 3 and 4 at the time interval favorable for actinomycetic growth. In both series, the data show the marine actinomycetes more susceptible at lower concentrations than were the marine bacteria.

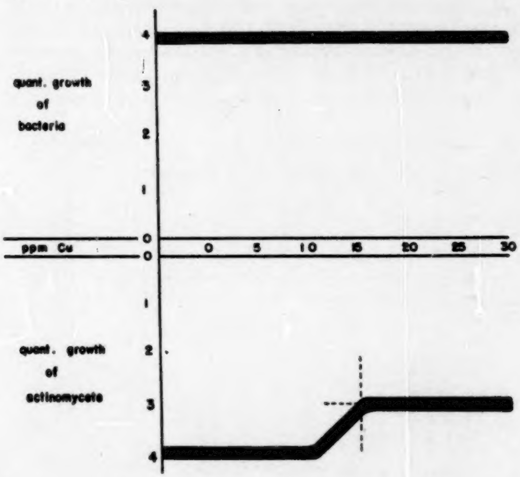

Fig. 4.—Response of selected marine actinomycetes and bacteria to varying concentrations of Cu. Differences in response are based on a 5-point qualitative scale. Note that the reverse desired effect is obtained as far as isolation procedure is concerned in that bacterial competition is not reduced but favored.

A preliminary check on the activity of antibiotics as differential inhibitors was carried out by swabbing twelve plates, six each, with both a mixture of spores from known isolates and with a 1:100 diluted sample from which actinomycetes had been isolated previously. The antibiotics used, their concentrations and the results, as measured by the diameter of the inhibition ring in mm, are shown in Figure 5. In all instances the actinomycetic mixture was more sensitive to the antibiotic than were the marine bacteria. In a second series of tests, a large number of samples were diluted 1:100 and one series treated with 2.5 units per ml of streptomycin and a second series with 20 units of penicillin per ml of diluted sample. Again, no new actinomycetes were recovered and the purified marine isolates were found to be more susceptible to these two antibiotics than were the bacteria of the samples.

Forty-five purified amino acids and carbohydrates were made up as sea water agars and treated with diluted sample in the same manner as the desiccation plates. It was hoped that one of them would prove to be a differential medium which would constitute an ideal means of isolation technique. In addition, a series of semisynthetic agars were made up using complex marine materials. The synthetic and semisynthetic series were run concurrently with the regular desiccation series so that comparative checks could be made and differences spotted easily. One series of 35 samples showed a 17 percent increase on DL-phenylalanine over a desiccation series of the same samples. Inasmuch as these results could not be reduplicated later on, this agar cannot be designated as differential.

The first 75 marine actinomycetic isolations represented approximately a 5 percent yield from the sampling. This is far below that obtained by Grein and Meyers (1959) with a caesin-starch isolation

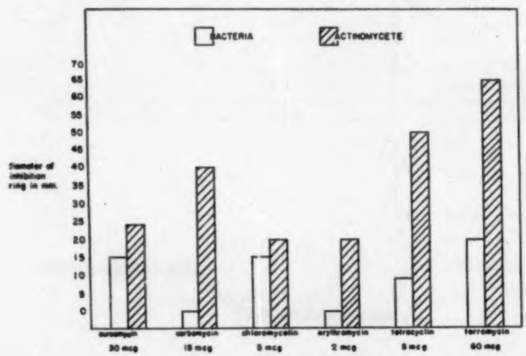

Fig. 5—Differential response of selected marine actinomycetes and bacteria to various antibiotics. Note in each case that the bacteria are more resistant.

agar. Analyses of the disposition of these isolates as to area, substrate, and response to gross salinities are illustrated in Figures 6 and 7.

In Figure 6-A, the number of isolates obtained from each area is indicated as a percentage of the total number of samples collected from the stations of the area. The greater concentration of actinomycetes were in the Aransas Bay and the Matagorda Bay areas. Since the areas were chosen as arbitrary sections of the coast, these data are relevant only to depict a real distribution along the coast. In part D of Figure 6, the isolations are plotted as percentages of the total. These data show that the greatest recovery was from the Aransas Bay and the Matagorda Bay areas. When compared with the sample yield data for the same areas in part A, it is evident that a greater number of isolates was obtained in fewer samples from the Matagorda stations.

In Figure 7-A, the isolates are plotted as to type of substrate they were obtained from as a percentage of the total. The decreasing order from organic substrate to mud to water to sand is to be expected on the basis of relative amounts of available nutrients. In part B of Figure 7, it is interesting to note that 83 percent of the isolates were obtained from hyposaline waters. On the other hand 17 percent of the isolates were obtained from gulf waters and none from the hypersaline bays. A comparison of these two latter broad habitats is probably not significant since there is quite a discrepancy in the number of samples between the two. The surf stations were easily accessible all along the coast; whereas, Baffin Bay was the only representative area collected on the hypersaline Leguna Madre. In addition, the failure to recover isolates from the hypersaline stations is not explainable in

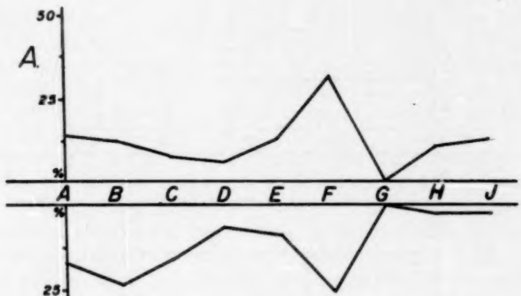

Fig. 6.—Station sampling yields. A-isolates obtained/ number of station samples; B-isolates obtained/total number of isolates. For sampling areas, *vide* Figure 1.

terms of adaptibility to high salinity as the isolates will grow or tolerate enriched media with salinities of 60 or even 90 ppt. The difference between the yields from polluted and nonpolluted hyposaline substrates is probably not significant.

In the evaluation of the above data, the question arises naturally as to: (1) the disposition of the different phases of the life cycle within the natural environment; and (2) the degree of adaptation of actinomycetes in the marine habitat. These two phases are closely related. For example, Waksman (1934, 1950, 1957) has stated that actinomycetes are absent from the marine habitat with the exception of those that are washed from the soil, down the rivers, and into the oceans. Initially, the limited data of part B, Figure 7 would appear to support his thesis. We know that within the restricted and abnormal environment of a test tube of broth the spores and primary mycelium are microaerophilic and the more physiologically active secondary mycelium is aerobic, but requires some dehydration in order to sporulate. These conditions would be admirably met in a soil which is quite often a microaquatic habitat.

In a broad sense, terrestrial versus aquatic habitat differentiation, as it is commonly considered, may not exist at a microorganismal level. The difference is apparent as indicated by higher organisms on a basis of structural adaptation to desiccation and over a seasonal time scale — the greater the water conservational tissue organization

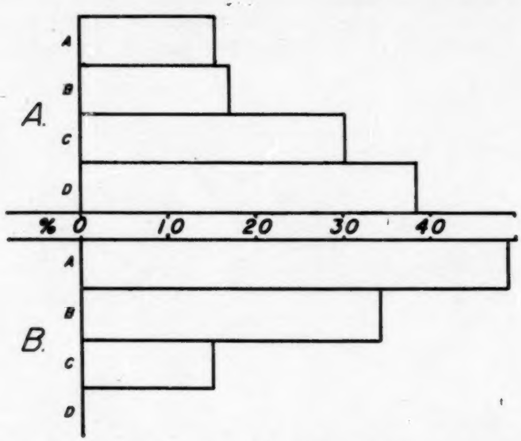

Fig. 7.—Analysis of isolates obtained/total number of isolates from gross substrates and salinities. They are for the substrates of A; A—sand; B—water; C—mud; D—organic material. They are for salinities or B: A—unpolluted hyposaline material; B—polluted hyposaline material; C—surf materials; D—hypersaline materials.

the longer their growing season in the harsh terrestrial environment. Of course, thalloid cryptogams lacking a complex arrangement for the prevention of desiccation can only exist where, such as in bodies of water, there is no loss of cellular moisture. Thus in the terrestrial environment, they must complete their life cycle at those times the habitat is aquatic and remain dormant for the remainder of what is the growing season for more complex plants.

Even if, on the other hand, there are no gross adaptational differences other than time of growing season between terrestrial and fresh water actinomycetic environments, one would expect in the marine habitat, discounting the large dilution factor plus the "sterilization effect of the sea" (Browne, 1917; Burke and Baird, 1931), the spore stage to be predominant and equally isolated regardless of the type of substrate. The greater occurrence of these marine isolates in organic materials indicates a completion of at least a portion of the life cycle in the marine habitat. In addition, it should be remembered that other investigators, referred to earlier in this paper, have isolated actinomycetes from areas reasonably free from terrigenous contamination.

The resolution of this question undoubtedly lies in final taxonomic analyses. However, species designated as soil actinomycetes, may become adapted to the marine habitat and even show morphological difference. Probably the question is not an important one for the simple reason the actinomycetes that occur in marine substrates are evidently well adapted and carry on the same activities as do those of other habitats. The degree that these activities differ, as modified by the very different type of communal life, is the important aspect of these studies.

The mechanism of adaptation to the marine environment might be further elucidated in terms of response to various salt concentrations. The concept of endemism in a holocoenosis is a familiar one and there are many examples of such narrowly restricted organisms. Flannery (1956) sought a critical concentration with which he could divide microorganisms on the basis of their tolerances to salinity. He selected 2 percent salt as this limit and classified those organisms that would grow in media containing less than 2 percent salt as salt-sensitive nonhalophiles (obligate glykophytes). If organisms would grow in media containing more than 2 percent salt he called them salt-tolerant nonhalophiles (facultative glykophytes). Those organisms that grow only in a medium containing more than 2 percent salt were designated as obligate halophiles and those that grow only in a medium containing less than 2 percent salt as facultative halophiles.

The findings of ZoBell and Michner (1938) seem to refute the inference that there is a cut-and-dried response to salt concentration. These investigators completed a series of studies in which they started with twelve obligate marine bacteria on a medium containing 75 percent sea water. When the cultures reached maximum growth, they

were transferred onto a medium containing 5 percent less of sea water. Five of the twelve bacteria grew in concentrations of 5 and 10 percent of sea water in the final transplant. None of these forms showed any morphological alteration. After five months all but three of the twelve would grow in a medium containing a concentration of 10 percent of sea water.

Four months after the initiation of this study, the first twenty isolates were plated out, each on a series of ten plates containing progressively 10 percent less of sea water. Eighty percent of the 20 forms grew only on the 80 percent, 90 percent and full strength sea water plates. These could be designated as obligate halophytes as an 80 percent of sea water plate would be well above a 2 percent salt concentration. It was interesting to note that the remaining 20 percent, not strictly obligate halophytes or faculatative halophytes, were the oldest isolates. A few months later a like series was repeated on 30 isolates, and only those that had been isolated in the last two months could be designated as obligate halophytes. A recent series of 60 isolates was run in which the salinities of the media were 19, 25, 34, 68, and 136 ppt. Sixty-three percent of the forms grew best on the media containing 34 ppt or more, but would grow on plates with lower salinities. The remainder grew best at the lower salinities but would grow on all salt concentrations and would be designated as facultative glykophytes.

These data seem to agree with the opinions of ZoBell and Michner (1938) who explain their results on the theory that senescence increases tolerance whereas recent transfer or isolation tends to narrow the tolerance spectrum.

SUMMARY

The unique barrier bar-lagoon hydrographic relationships of the Texas Gulf Coast are described as they pertain to the production of potential actinomycetic populations.

Seventy-five isolates of marine actinomycetes were obtained from thirty-nine sampling stations. These stations are described as to physical features and types of substrates sampled. The majority of the stations were located in the lagoons which are hypo- and hyper-saline and also serve as marine debris and human waste traps.

Isolation was achieved through a differential response of actinomycetes to low water tensions. Actinomycete colonies appeared following the bloom of bacterial colonies, apparently because of a competitive release, on Emerson's agar sea water plates. Differential selection with bacteriostatic or -cidal compounds was not accomplished as the actinomycetes were more susceptible than most of the bacterial flora.

The isolate sample yield was five percent. The greater percentage of isolates was obtained from the Matagorda and Aransas Bay areas. The Matagorda isolates were obtained from fewer samples. No isolates were obtained from the hypersaline (*ca.* 70 ppt) southern bays. Thirty-eight percent of the isolates were recovered from organic substrates,

thirty percent from sand. Forty-eight percent of the isolates were recovered from the relatively unpolluted hyposaline stations, thirty-seven percent from hyposaline stations polluted with sewage and chemical wastes, fifteen percent from Gulf stations and zero percent from hypersaline stations.

The controversy of whether or not actinomycetes recovered from marine substrates are true habitat forms (in this case, halophytes) or washed-in glykophytes is discussed. Approximately eighty percent of the isolates could be classified as obligate halophytes at initial isolation. After several months of growth on artificial media, their tolerance spectrum widened so that they could be classified as facultative halophytes to facultative glykophytes.

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Lupinus pusillus and Its Relationship

DAVID B. DUNN
University of Missouri, Columbia

The taxa here treated as belonging to the species *Lupinus pusillus* Pursh have previously been treated by some authors as distinct species and by others as varieties. The three have not previously been placed together as a complex species. The relationship was recognized while the treatment of *Lupinus* was being prepared for the *Leguminosae* Part II, *Lupinus,* for *Contributions Toward a Flora of Nevada.* The necessary name changes were made in *Leaflets of Western Botany* 7:255, 1955, so that the names could be employed in the Nevada Flora. It has not been possible to follow through with a monographic analysis and a detailed explanation of why the three are considered to be conspecific, until now.

Lupinus pusillus belongs to that relatively small group of annual lupines which have sessile, connate cotyledons, the leaflets elliptical to oblanceolate, conduplicate and glabrous above, a glabrous corolla, and generally only two ovules in the pods. The species appears to form a geographic ring structure such as referred to by Goldschmidt (1952: 90) with the subspecies at the opposite ends nearly sterile but apparently breeding readily with the intermediate subspecies. This observation is based on the study of herbarium material which shows intermediate morphology in the intermediate geographic areas. These have been plotted as putative hybrids on the distribution map (Fig. 3). Three successive attempts have been made to grow the three subspecies since 1955 but it has not been possible to keep them growing long enough to bring them into flower, to demonstrate the degree of interfertility, in the laboratory. Even so, I believe that the data shown in Figure 1, the chart of the floral parts, drawn to the mean valves of a random series of 25 measurements, and the pictorialized diagram in Figure 2, adequately bear out my interpretation.

At the southern end of the Great Basin in Nevada, Utah, and Arizona (see Figs. 1, 2, & 3) the subspecies *rubens* forms one end of the chain. Subspecies *rubens* shows either introgression from *Lupinus odoratus* or common ancestors which introgressed. The deep blue color of the wings, inflated wings, the orbicular banner, the glabrous base of the calyx and pedicel all bear out the relationship between them. These characters led W. L. Jepson to suggest that the taxon *rubens* should be treated as a variety of *L. odoratus* Hel. This suggestion ignores the fact that *L. odoratus* is acaulescent, has glabrous pods, except along the sutures, has 4-6 ovules per pod and the seeds are quite different. In all of these latter characters, subsp. *rubens* is conspecific with *L. pusillus.* In addition, as specimens are studied from areas fur-

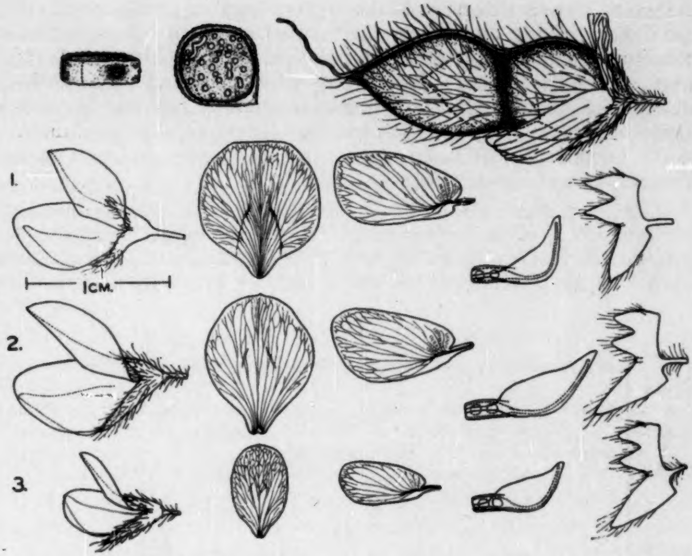

Fig. 1.—Illustrated chart of the floral, pod and seed characteristics of *Lupinus pusillus.* The floral parts are drawn to scale for the mean values of a random sample of 25 plants. The typical conformation of each part is shown: Subspecies *pusillus* (2), subspecies *rubens* (1) and subspecies *intermontanus* (3). The dotted lines on the pod and seed illustrations show the extent of variation of the respective parts in size. Top row, left to right, edge view of seed, side view of seed, left lateral view of pod. The floral parts in rows 2-4 are, left to right, side view of intact flower, banner flattened, side view of wing, side view of keel, and ventral view of the unfolded calyx cut along the left lateral sinus.

ther east within the range of subsp. *rubens,* the floral characters become more and more like those of typical *L. pusillus* with the glabrous base of the calyx being the last character to disappear, so that the population must be treated as typical *L. pusillus* near the western state line of Colorado. Only an occasional plant shows intermediacy between subspecies *rubens* and subspecies *intermontanus* although typical material of subspecies *intermontainous* extends from Washington through the entire Great Basin and into Arizona. Thus, the suggestion that *L. pusillus* may represent an example of a species ring as described by Goldschmidt is made.

Lupinus pusillus subspecies *pusillus* is relatively uniform extending from New Mexico to Canada in sparse grassland and into montane valleys along the Rocky Mountains. In Wyoming the plants show progressively more characteristics of subspecies *intermontainous* toward

the west. The specimens in Idaho represent either transplanted material due to driving stock along the Snake River route of migration or possibly a natural finger of the population resulting from interlocking areas of natural habitat. The former view is favored particularly in view of the recent evidence of transplantation of *Lupinus nanus* subspecies *menkerae* from the southern San Joaquin Valley in California to the northern Great Basin, apparently by hauling livestock to and from winter and summer grazing areas.

Lupinus pusillus subspecies *intermontainous,* as mentioned, blends into typical *L. pusillus* in Wyoming. In its more typical morphological condition in Nevada and elsewhere, it is characterized by the virtual absence of the peduncle, hence sessile racemes, generally not equalling

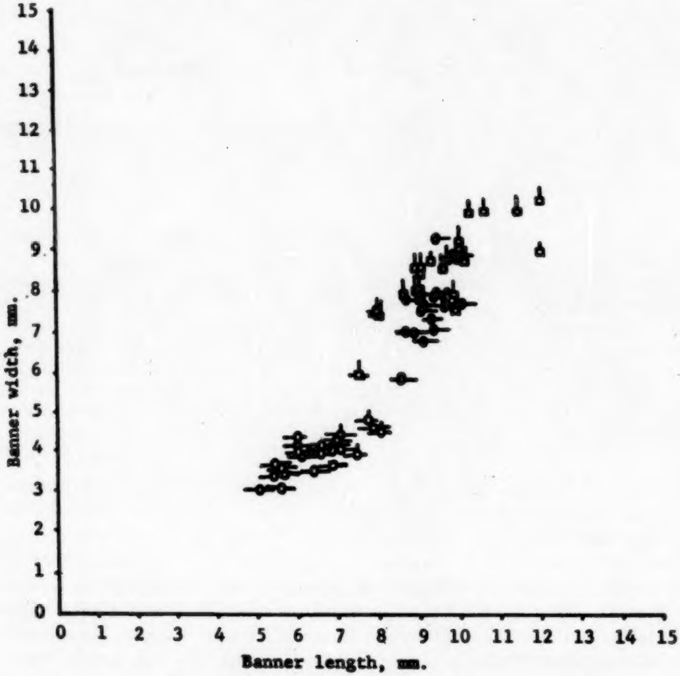

Fig. 2.—Pictorialized diagram for five characteristics of the subspecies of *Lupinus pusillus.* Subspecies *pusillus* (●), subspecies *rubens* (□) and subspecies *intermontanus* (O). 1) Racemes shorter than foliage —O, intermediate –O, exceeding foliage O. 2) Petals deep, rich, blue color (O, with long line above), intermediate (O, with short line above), pale blue to nearly white (O). 3) Basal, fused part of calyx hairy O—, intermediate O–, glabrous O.

the foliage, and much smaller flowers, as shown in Figures 1 and 2. The sessile nature of the raceme is found in several other species of the Great Basin and the Northwestern United States. It is general for *L. cusickii* and *L. caespitosus* both perennials. It occurs fairly commonly in *L. kingii,* an annual. Occasionally the sessile raceme may appear in *L. brevicaulis,* a small annual seldom over 2-3 inches tall. The prevalence of this characteristic among several taxa in the northern Great Basin suggests introgression or common, ancestors in that area in the past, also suggesting the other end of the chain of three subspecies. The unusual concave sides of the seeds with ridges and an irregular marginal rim, strongly or weakly developed, are so unusual in the genus *Lupinus* that the affinity of the three subspecies can hardly be doubted.

KEY TO SUBSPECIES OF LUPINUS PUSILLUS AND THEIR ALLIES

1. Leaflets pubescent above; perennial; densely caespitose tuffed from a caudex; ovules 2-6, generally 3-4 seeds, ovoid, the sides convex ...... (those perennial species of the northern Great Basin with which the subsp. of *L. pusillus* could be confused, *L. volutans, L. caespitosus, L. aridus,* & *L. cusiskii*)

1. Leaflets glabrous above; annual; simple or branched without a caudex. ....(2)

2. Ovules 4-6; plants glabrous except the sutures of the pods; acaulescent. ....*L. odoratus*

2. Ovules generally 2, rarely 3; variously pubescent; caulescent, sometimes stems only 1-3 cm long. ....(3)

3. Stems covered with a close, felt like, pubescence, no spreading hairs present (restricted to W. Nev. & Calif. deserts). ....*L. shockleyi*

3. Stems with hirsute or pilose spreading hairs, often quite sparse. ....(4)

4. Flowers borne in compact, headlike racemes, generally 2-2.5 cm long, pedunculate or occasionally sessile. ....*L. kingii*

4. Flowers borne in lax elongate racemes, or 3 cm or more long. ....(5)

5. Peduncles obsolete, rarely as much as 1 cm. long; inflorescence shorter than the leaves; plants coarsely spreading, hairy; banner less than 5 mm wide. ....*L. pusillus* subsp. *intermontanus*

5. Peduncles evident; inflorescence exceeding the foliage, sometimes only slightly; banner 6-10 mm wide. ....(6)

6. Peduncles 3-6 cm long, decumbent or erect; racemes dense; mature pods ovoid, 5-6 mm wide, margins flat, not constricted between the seeds, sparsely pubescent on the sides; generally interpreted as acaulescent (Nevada & Calif.). ....*L. flavoculatus*

6. Peduncles 1-3.5 cm long, erect; racemes lax; mature pods 6-7 mm wide, torulose, abundantly pubescent, distinctly caulescent. ....(7)

7. Calyx cup and pedicel glabrous, only the teeth with some hairs; corolla commonly deep blue; wings often appear inflated and stand wide apart along the top side. ....*L. pusillus* subsp. *rubens*

7. Calyx cup and pedicel pilose to hirsute; corolla pale blue to white; wings appear to lie rather close to the keel, the upper margins generally touching most of their length. ....*L. pusillus* subsp. *pusillus*

Lupinus pusillus Pursh subsp. *pusillus,* Fl. Am. Sept. 2:468. 1814.

Plants annual, 8-20 cm tall, simple or diffusely branched from the lower nodes; cotyledons sessile, connate-perfoliate; stems distinctly present, the internodes 1-2 cm long, except the first internode of each branch, which is 2-5 cm long at maturity, densely pilose to hirsute, the hairs 2-3.5 mm long, commonly flat and twisted; mature petioles 2-5.5 cm long, similarly pubescent; lower stipules 6-8 mm long, connate to the petiole 5-6 mm; leaflets 6-8, glabrous above, marginal hairs may fold inward on drying, the largest leaflets 1.5-3.5 cm long, 4-8 mm wide, oblanceolate, the tips obtuse; peduncles 1-2 cm long; racemes 3-5 cm long, exceeding the foliage, lax, the flowers scattered; bracts persistent, subulate, 2-4 mm long, pilose; pedicels 1-2 mm long at anthesis and 2.5-3.5 mm long at fruiting, thinly pilose; calyx thinly pilose to hirsute on the outer surface; corolla glabrous; banner obovate to suborbicular, reflexed near the midpoint, pale blue to white, cream, lavender or pink, sometimes darker blue particularly in the region of intergradation with subsp. *rubens,* 8.6-10 mm long, 7-8.8 mm wide; wings 8.6-10.4 mm long, 3.5-5 mm wide; keel

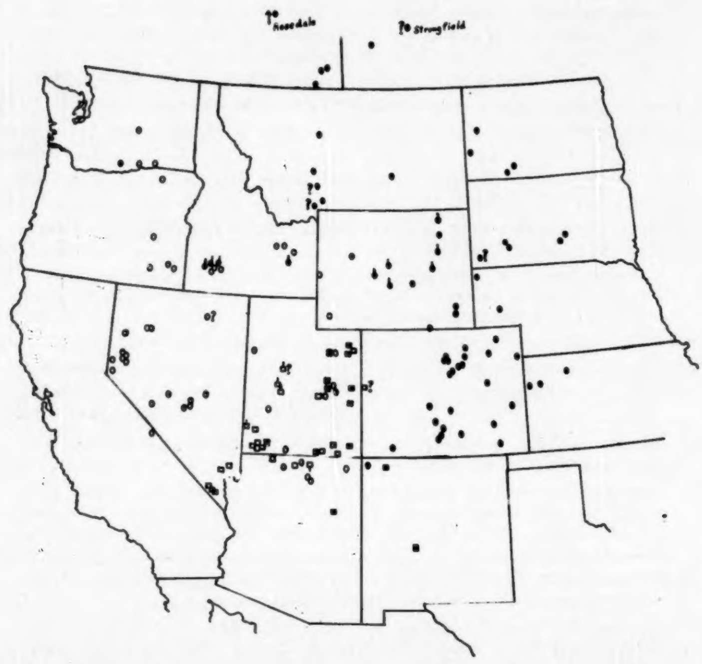

Fig. 3.—Distribution map of *Lupinus pusillus:* Subspecies *pusillus* (●), subspecies *rubens* (□) and subspecies *intermontanus* (O). A "?" indicates that the exact location was not found on the available maps. The putative hybrids or intermediates (●, □ with tails, and half solid squares).

glabrous, lavender near the acumen; pods 14-18 mm long, 6-7 mm wide at the seeds, torulose, sparsely to abundantly hirsute to pilose, the hairs often flat and twisted; the seeds two, white, cream or pastel green with flattened rugose sides and a raised marginal ridge or rim, so the sides are convex.

The original description by Pursh was made from a specimen collected by Merriweather Lewis on the banks of the Missouri. This specimen was not seen but both a specimen collected by Nuttall on the banks of the Missouri, supposedly near the White River, as noted by Heller (1909) and a specimen from near the White River on the upper Missouri River collected by Geyer in 1839 were seen. All of the Missouri River drainage is within the distribution of the material interpreted as being *L. pusillus* subsp. *pusillus,* so it is hardly possible that material of one of the other two subspecies could have been used in the original description. Douglas' specimen in the Lindley Herbarium, which was used by Hooker (1830) and Agardh (1835) to describe *L. pusillus* was seen and was material of the subsp. *intermontanus* and has been so annotated. Torrey and Gray (1840) used Lewis' and Nuttall's specimens for their description.

Partial Citation of Representative Material

COLORADO. Lat. 40-41° Powell's Exp. *Geo. Vasey* 103 yr. 1868 (MO). Upper Arkansas, *D. Torrey* July 1867 (MO). ADAMS CO: Aurora, *J. A. Ewan* 14410 (COLO). Wheeler's Expd. *Wall & Rothrock* 198 (PH). Denver, *I. W. Clokey* 3079 (UC, CAS); *Eastwood* May 1887 (COLO). ALAMOSA CO: Alamosa, *F. Ramaley* 12012 (COLO). Great Sand Dunes Nat. Mon. *A. M. Alexander* 166 (UC), BOULDER CO: Boulder, *A. G. Vestal* June 1915 (DS). White Rocks, *W. A. Weber* 3726 (COLO); *F. Ramaley* 11575 (COLO); *J. Ewan* 11908 (COLO); *F. Ramaley* 1003 (COLO). CHAFFEE CO: *C. P. Smith* 3910 (DS, POM); *C. F. Baker,* yr. 1903 (POM). ELBERT CO: Limon, *Marion Ownbey* 1300 (MO). EL PASO CO: East of Colorado Springs, *Shoop* 242 (UMO); *T. C. Porter,* Aug. 1873 (PH). FREMONT CO: Canon City, *T. B. Brandegee* 11 (UC, MO); *A. Nelson* 10499 (UC, MO). HUERFANO CO: Walsenburg, *A. G. Vestal* 391 (DS). JEFFERSON CO: Clear Creek, Denver, *I. W. Clokey* 4192 (UC, MO, PH). KIOWA CO: Rush Creek, *L. Williams* 2290a (UC, MO). LA PLATA CO: Durango, *H. L. Sumner* June 20, 1952 (COLO). LAS ANIMAS CO: West of Baca Co. line, *C. M. Rogers* 6005 (COLO). LINCOLN CO: Limon, *F. Ramaley & Gambell* 16078 (COLO). LOGAN CO: W. Sterling *M. E. Mathias* 352 (POM, MO). MORGAN CO: Brush, *F. Ramaley & W. G. Gambell* 16007 (MO, COLO); *E. Ramaley* 16362 (COLO). OTERO CO: La-Junta, *LoPaull* 19 (COLO). SAGUACHE CO: Crestone, *F. Ramaley & K. R. Johnson* 14640 (COLO); 14859 (UC, COLO). Great Sand Dunes Nat. Mon., *H. L. Zobel* Sept. 1, 1939 (CAS); *G. T. Bean* 51-40 (COLO). WELD CO: Greeley, *M. E. Jones* June 20, 1925 (Intermediate or aberrant) (POM); *E. C. Smith* May 10, 1891 (MO). Hudson, *F. Ramaley* 11369 (COLO). New Windsor, *Osterhaut* June 1901 (PH). Roggen, *F. Ramaley* 11805 (COLO); 12340 (COLO); 15318 (COLO). YUMA CO: Wray, *W. W. Eggleston* 15158 (Flrs. small) (POM, MO).

IDAHO. BINGHAM CO: Blackfoot, *M. E. Jones* July 7, 1909 (POM). ELMORE CO: Hammett, *H. D. Ripley & R. C. Barneby* 6482 (CAS). GOODING CO:

Hagerman, *Shoop* 142 (UMO). OWYHEE CO: Grand View, *B. Maguire* & *A. H. Holmgren* 26212 (DS, UC, COLO). 7 mi. N.E. Bruneau, *B. Maguire* & *A. H. Holmgren* 26265 (UC) (intermediate to subsp. *intermontanus*).

KANSAS. GRAHAM CO: Sandy soil, *A. S. Hitchcock* 81-a July 20, 1897 (MO). LOGAN CO: Sandy soil, *A. S. Hitchcock* 81 May 11, 1895. WALLACE CO: *W. A. Kellerman* July 5, 1885 (MO, UMO).

MONTANA. CASCADE CO: Falls of Missouri, *Forest* Sept. 1886 (UC). Headwaters Missouri & Yellowstone Rivers, *F. V. Hayden* 1859-1860 (MO). Upper Missouri, *Culbertson* 1850 (PH). Yellowstone, *J. W. Blankinship* July 3, 1899 (MO). YELLOWSTONE CO: Custer, *J. W. Blankinship* 150 May 28, 1890 (UC, MO).

NEBRASKA. Between South Platte & Pole Creek, *H. Engelmann* July 1856 (MO). Badlands, *F. V. Hayden* July 2, 1855 (MO, PH). Platte River, *H. Engelmann* July 11, 1858-9 (MO). MORRILL CO: Broadwaters, *H. Hapeman*, July 11, 1935 (UC, UMO). Mauvaises Terrs., *F. V. Hayden* June 1853 (MO). SIOUX CO: Harrison, *H. D. Ripley* & *R. C. Barneby* 9110 (CAS). In prairies, *Joseph Kramer* 43 (MO). Fort Laramer, *F. V. Hayden* 1853-4 (MO).

NEW MEXICO. Lock, *C. Wright* 1362 yr. 1852 (PH) (shows intermediacy to subsp. *rubens*). SAN JUAN CO: Bloomfield, *H. D. Ripley* & *R. C. Barneby* 8376 (CAS) (with some drift toward *rubens*). 17 mi. S. of Shiprock, *H. D. Ripley* & *R. C. Barneby* 5284 (CAS) (with some drift toward *rubens*).

NORTH DAKOTA. GOLDEN VALLEY CO: Sentinel Butte, *H. C. Hanson* June 17, 1934 (UC). GRANT CO: Wade, *D. B. Bell* 21 (UC). Cannon Ball, *H. F. Bergman* 1860 (MO). MCKENZIE CO: N. Roosevelt Park, *O. A. Stevens* 724 (UC, MO).

SOUTH DAKOTA. "Bad Lands," bottom of Little Missouri River, *Wm. M. Canby* 108 July 27, 1883 (PH). Interior, *W. H. Over* 6123 (COLO). Chamberlain, *E. N. Wilcox* Aug. 1892 (MO). WASHABAUGH CO: Pine Ridge Indian Res. 10 mi. S. of Interior, *E. J. Palmer* 37632 (MO). COUNTY? Near White River upper Missouri River, Nicollets Northwest Exp. June 6, 1839, *Chas. A. Geyer* 151 (MO). "Missouri," *Nuttall* (PH).

UTAH. EMERY CO: Green River, *M. E. Jones* May 23, 1895 (UC); May 8, 1890 (UC) (both inter. to subsp. *rubens*).

WYOMING. CAMPBELL CO: Between Douglas & Gillette, *C. L. Porter* 3952 (DS, UC). Spotted Horse, *Fassett* June 22, 1941 (WIS). CONVERSE CO: Glenrock, *B. W. Evermann* July 14, 1893 (DS). FREMONT CO: Moneta, *C. L. Porter* 5742 (DS, UC, RSA, MO, PH) (intermediate to subsp. *intermontanus*). Between Muddy Gap and Lander, *C. L. Porter* 4943 (DS, UC, COLO, RSA, PH) (some specimens suggests intermediacy to *intermontanus*). Sweetwater River, *E. Nelson* 4989 (POM) (some traits of *intermontanus*). LARAMIE CO: Wheatland, *A. Nelson* 8258 (DS, UC, POM, MO). NATRONA CO: Alcova, *L. N. Gooding* 157 (UC, POM, MO); *C. L. Porter* 4863 (RSA). PLATTE CO: 5 mi. N. of Wheatland, *C. L. Porter* 3544 (DS, UC, MO). Colorado-Wyoming boundary, Lat. 41°, Am. Plains Flora, *E. Hall* & *J. P. Harlour* 1862 (POM, MO, PH).

STATE & COUNTY? Fort Wallace, *C. C. Parry*, June 1867 (MO); *Wm. A. Bell*, 1867 (PH).

CANADA. ALBERTA: Lost River, Manyberries, *D. Manske*, July 12, 1935 (DAO). Manyberries, *H. Groh*, June 9, 1931 (DAO); *E. H. Moss* & *Campbell* 9796 (DAO). Milk River Valley, *J. A. Campbell* 42 (DAO). Rosedale, *M. E. Moodie* 946 (DS, UC, MO).

SASKATCHEWAN: Beverly, *A. J. Breitung* 5841 (DAO). Strongfield, *R. C. Russell* 3756 (DAO).

Lupinus pusillus subsp. *intermontanus* (Heller) Dunn

Lupinus intermontanus Heller. Muhl. 8:87. 1912.
Lupinus pusillus var. *intermontanus* (Heller) C. P. Smith. Bull. Torr. Bot. Club 46:408. 1919.
Lupinus pusillus subsp. *intermontanus* (Heller) Dunn. Leafl. West Bot. 7:255. 1955.

Plants annual, 6-15 cm tall, simple or diffusely branched from the lower nodes; cotyledons sessile, connate-perfoliate; stems developed, the internodes 0.5-1 cm long, except the first internode of each branch 2-4.5 cm long at maturity, with sparse to ample pilose to hirsute hairs 2.5-3.5 mm long, somewhat flattened and twisted on herbarium material; mature petioles 3-6 cm long, similarly pubescent; lower stipule 12-20 mm long, connate to the petiole 10-15 mm; leaflets 5-6, glabrous above, oblanceolate-oblong, the tips rounded, obtuse or acute, the largest 2-3 cm long, 5-10 mm wide; peduncles obsolete, sometimes 3-8 mm long; racemes 2-5 cm long, usually dense and included within the foliage often 2-5 cm shorter than the leaves; bracts persistent; subulate; pedicels 1 mm long in flower, 2 mm long at fruit sparsely pilose; calyx glabrate to very sparsely pilose below, with more numerous hairs on the outer portion of the lips; corolla glabrous generally white or green or with a lavender tint; the banner oblong to obovate, reflexed near the mid-point, 5-8 mm long (ave. 6.4 mm), 3.0-4.7 mm wide; wings 5.5-7.5 mm long (rarely 9 mm long and then probably intermediate, ave. 6.9 mm long) 2.5-3.5 mm wide; keel glabrous; pods 16-20 mm long, 5.5-7 mm wide, torulose, hirsute-pilose, usually two seeded; seeds flattened, rugose, with a marginal ridge, nearly round, 3.7 x 4 to 5.3 x 5-6 mm, commonly white.

The specimen used by Heller (1909) for his description of *L. pusillus* was subsp. *intermontanus* and hence variation from previous descriptions. Heller noted a mixture of specimens of subspecies *intermontanus* and *subsp. rubens* on the same herbarium sheet but from different collectors. It is not uncommon to find specimens of *L. kingii* also mounted on the same sheet without the collector or mounter apparently being aware of the difference.

PARTIAL CITATION OF REPRESENTATIVE MATERIAL

ARIZONA. APACHE CO: Rock Point, *H. C. Cutler* 2189 (CAS, MO) (intermediate to subsp. *rubens*). COCONINO CO: Moenkopi, *M. E. Jones* June 10, 1890 (POM). Lee's Ferry, *M. E. Jones* June 12, 1890 (POM). Jacob's Pool, *M. E. Jones* June 1890 (POM). Tuba City, *R. H. Peebles* & *E. G. Smith* 13358 (CAS).

CALIFORNIA. INYO CO: Deep Springs Valley, *C. A. Purpus* 5807 (UC).

IDAHO. BONNEVILLE CO: Idaho Falls, *A. Nelson* 10068 (UC, MO). BUTTE CO: Howe, *C. L. Hitchcock, Rethke, & van Roadshooven* 3822 (CAS). ELMORE CO: Glenn's Ferry, June 17, 1911 (POM). JEFFERSON CO: 10 mi. NE. of Howe, *C. L. Hitchcock* 15752 (DS, UC, RSA). OWYHEE CO: Bruneau, *M. E. Jones* June 23, 1930 (POM). 11 mi. S. of Bruneau, *R. J. Davis* June 10, 1939 (CAS).

MONTANA. Blackfoot River, *J. M. Coulter* July 1872 (PH).

NEVADA. Nevada Plains, *G. Engelmann* July 2, 1880 (MO). ELKO CO: Columbus, *M. E. Jones* May 20, 1897 (POM). ESMERALDA CO: *Candelaria, W. H. Shockley* 270 (UC). HUMBOLT CO: NE. of Jungo, *J. P. Hester* 1219 (RSA). HUMBOLT-PERSHING CO: Rose Creek, *M. E. Jones* June 16, 1901 (POM). LYON CO: Fernley, *L. Benson* 6711 (POM). NYE CO: Warm Springs, *B. Maguire & A. H. Holmgren* 25356 (CAS, UC, DS, MO, PH). 15 mi. N., *B. Maguire & A. H. Holmgren* 25140 (DS, CAS, UC). 10 mi. W., *A. Eastwood & J. T. Howell* 9456 (CAS). Callaway, *H. D. Ripley & R. C. Barneby* 3629 (CAS). ORMSBY CO: Empire City, *M. E. Jones* 3813 (POM, MO); *M. E. Jones* July 19, 1882 (DS, CAS, POM, UC). Lodi Valley, North of Gabbs, *B. Maguire & A. H. Holmgren* 25494 (UC). PERSHING CO: *H. D. Ripley & R. C. Barneby* 4549 (CAS). Imlay to Jungo, *A. Alexander & L. Kellogg* 4618 (DS, UC). Rawhide Jct., *B. Maguire & A. H. Holmgren* 25437 (CAS, DS, UC). WASHOE CO: Wadsworth, *A. A. Heller* 9599 (Type & Isos Nev. Agr. Ex. Sta.) (POM, DS, UC, MO, PH); *P. B. Kennedy* 2052 (Topotype, DS); *W. A. Archer* 6205 (UC, DS); *K. Brandegee* 2052K. (UC). Reno, *F. H. Hillman* (POM No. 23608).

OREGON. HARNEY CO: Alvord desert, *Wm. C. Cusick* 2020 (UC, MO). Drew's Valley, *Mrs. R. M. Austin,* July 1893, (UC). MALHEUR CO: Rome, *M. E. Peck* 21781 (CAS, DS). Rome, sand bluffs, Owyhee River, *H. D. Ripley & R. C. Barneby* 6158 (CAS). UMATILLA CO: Umatilla, *M. E. Jones* June 1, 1905 (POM).

UTAH. BEAVER CO: Milford, *M. E. Jones* June 17, 1880 (POM). DUCHESNE CO: Theodore to Myton, *M. E. Jones* May 19, 1908 (POM) (in part). EMORY CO: Green River, *M. E. Jones* May 19, 1914 (POM); May 23, 1895 (POM). San Rafael Swell, *M. E. Jones* May 19, 1914 (DS, POM). KANE CO: Kanab, *M. E. Jones* 5286, May 22, 1894 (POM, UC). SALT LAKE CO: Salt Lakes, *T. Meehan* yr. 1883. SAN JUAN CO: Rainbow Bridge Trail, *J. T. Howell* 24669 (CAS). TOOELE CO: Dutch Mt., *M. E. Jones,* June 15, 1900 (POM). WEBER CO: Ogden, *T. C. Porter,* June 1871 (PH).

WASHINGTON. Washington Territory, *Wm. M. Canby* 706 yr. 1883 (UC). BENTON CO: Paterson, *B. F. Dona* June 8, 1950 (RSA). GRANT CO: Quincy, *J. W. Thompson* 9083 (POM, DS, UC, RSA, MO); 6760 (POM, DS, MO, PH). KLICKITAT CO: Bickleton, *Mrs. A. Gotfredson* 85 (POM). WALLA WALLA CO: Wallula, *F. Tweedy* May 1883 (DS); *J. S. Cotton* 1028 (MO).

WYOMING. FREMONT CO: Sandbar along Wind R. 13 mi. S. of Dubois, *C. L. Porter* 4244 (RSA). LINCOLN CO: Fairbanks (Prob. Fairview), *A. Nelson* 490 (UC) (intermediate to subsp. *pusillus*). UINTAH CO: Lyman, *H. D. Ripley & R. C. Barneby* 7853 (CAS).

Lupinus pusillus subsp. *rubens* (Rybd.) Dunn

Lupinus rubens Rybd. Bull. Torr. Bot. Club. 34:45. 1907.
Lupinus odoratus var. *rubens* (Rybd.) Jeps. Fl. Calif. 2:282. 1936.
Lupinus pusillus subsp. *rubens* (Rybd.) Dunn. Leafl. West Bot. 7:255. 1955.

Plants annual, 8-15 cm tall; cotyledons sessile, connate-perfoliate; stems distinct though short, the internodes usually less than 1 cm long except for the first internodes of the basal branches which are 3-4 cm long by maturity, with sparsely pilose to abundantly hirsute hairs 2-3.5 mm long; mature petioles 4-6 cm long, similarly hirsute; lower stipules 6-10 mm long, connate to the petiole

5-8 mm; leaflets 5-7, glabrous above, sparsely pilose to hirsute below, oblanceolate to spatulate, obtuse to rounded at the tip, the largest 1.5-2.5 cm long, 6-9 mm wide; peduncles 2-3.5 cm long, hirsute; racemes 6-10 cm long occasionally longer, exceeding the foliage, commonly lax, the flowers scattered; bracts persistent, subulate, 2-3 mm long, pilose hairy; pedicels 2-3 mm long at flowering, 3.5-5 mm long in fruit, typically glabrous but those from areas of intergradation have varying amounts of hair; calyx typically glabrous on the basal connate portion, with marginal hairs on the lips as well as some hairs inward on the lips; corolla glabrous; banner orbicular reflexed near the midpoint, generally a deep rich blue, but paler in areas with introgression, 7.5-12.0 mm long, 6.0-10.2 mm wide; wings 7.8-11.6 mm long, 3.0-4.8 mm wide, somewhat paler; keel pale lavender near the acumen; pods 15-18 mm long, 6-7 mm wider at the seeds, torulose, pilose with hairs 2-3 mm long; seeds normally 2, occasionally 3, white to cream or pastel greenish, the sides concave, rugose, also with a marginal rim.

This subspecies shows the deep blue flower color and sparser hairs which are undoubtedly due to gene flow from *L. odoratus.* The wider banner is also a character which tends to indicate this same affinity. *L. odoratus,* however, has pods with glabrous sides and 4-6 seeds and the pod is not torulose and the plants are acaulescent and nearly glabrous. The stem, pod, and seed characteristics of subsp. *rubens* are the same as those of subsp. *pusillus,* as well as, the leaves and pubescences. Hence, the interpretation that *rubens* is a subspecies of *pusillus* which has had some characters derived by gene flow from *L. odoratus.* While the interrelationship is obvious the question of whether subsp. *rubens* was a product of introgression between *L. pusillus* and *L. odoratus* at some point in the past or whether subsp. *rubens* represents an intermediate stage or link in a progressive stepwise pattern of evolution is not possible to state at present.

PARTIAL CITATION OF REPRESENTATIVE MATERIAL

ARIZONA. COCONINO CO: Navajo Springs, *M. E. Jones* 11704 (POM). Grand Canyon Bridge, *A. M. Alexander* 94 (UC). Endische Springs, *S. B. Benson* 163 (UC) (intermediate to subsp. *intermontanus*). MOJAVE CO: W. of Fredonia, *H. D. Ripley* & *R. C. Barneby* 8522 (CAS) (intermediate to subsp. *intermontanus*). NAVAJO CO: 20 mi. E. of Holbrook, *R. A. Darrow* July 8, 1940 (DS) (intermediate to subsp. *pusillus*). 1½ mi. N. of Navajo Bridge, *H. C. Cantelow* May 6, 1942 (CAS).

CALIFORNIA. ?

COLORADO. MESA CO: Chepeta Well, *M. E. Jones* 11542 (POM).

NEVADA. CLARK CO: East of Wilsons Ranch, *J. W. Clokey* 8711 (CAS, POM, DS, UC, MO); *I. W. Clokey* 8495 (UC). Crystal, *A. Eastwood* & *J. T. Howell* 9002 (CAS). Glendale, *R. J. Davis* 5045 (UC, RSA). Jean, *K. Brandegee* May 1915 (UC). Good Springs, *M. E. Jones* 11582 (POM). Dry Lake, *L. N. Gooding* 2234a (MO).

NEW MEXICO. DONA ANA CO: Near El Paso, *C. Wright* 1362 (MO) (intermediate material to subsp. *pusillus*). SOCORRO CO: San Antonio, *R. S. Ferris* & *C. D. Duncan* 2322 (DS) (intermediate with subsp. *pusillus*).

UTAH. DUCHESNE CO: Theodore to Myton, *M. E. Jones* May 19, 1908

(POM) (in part, intermediate to subsp. *pusillus*). EMERY CO: Woodside, *H. D. Ripley* & *R. C. Barneby* 8654 (CAS) (intermediate to subsp. *pusillus*); *M. E. Jones* May 23, 1395 (POM). Uteland Mine, Green River, *E. H. Graham* 8863 (MO). Green River, *M. E. Jones* May 9, 1890 (POM, DS, MO). San Rafael Swell, *M. E. Jones* May 19, 1914 (POM). 25 mi. S. of San Rafael, *B. Harrison* 7436 (MO) (intermediate to subsp. *pusillus*). GRAND CO: Cisco, *M. E. Jones* May 2, 1890 (POM) (intermediate to subsp. *pusillus*). Moab, *M. E. Jones* June 7, 1913 (POM) (intermediate to subsp. *pusillus*). IRON CO: Gold Hill, W. Utah, *M. E. Jones* 11565 (POM) (intermediate with subsp. *intermontanus*). Detroit, M. E. Jones 11564 (POM). JUAB CO: Champlin, *M. E. Jones* May 9, 1910 (POM) (intermediate to subsp. *intermontanus*). MILLARD CO: Deseret, *M. E. Jones* 11631 (POM) (part *L. Kingii;* top part intermediate with subsp. *intremontanus*). Tabernacle Crater W. of Meadow, *C. McMillan* 1428 (RSA) (intermediate to subsp. *intermontanus*). SAN JUAN CO: E. of Bluff, *A. H. Holmgren* 3181 (UC, MO, PH) (intermediate to subsp. *pusillus*). Copper Canyon, *Hugh C. Cutler* 2290 (CAS, MO) (some gene flow from subsp. *pusillus*). SW. of Mexican Hat, *A. H. Holmgren* 3246 (UC). Monument Valley, *A. H. Holmgren* & *S. Hansen* 3420 (UC, COLO, MO, PH). UINTAH CO: Vernal, *Louis Williams* 606 (CAS, MO, UC) (intermediate to subsp. *pusillus*). Ouray, *R. C. Rollins* 1732 (DS) (intermediate to subsp. *pusillus*). Dinosaur Monument Hdqrs., *W. A. Weber* 5428 (COLO); *R. A. Bradley* 5300 (COLO). WASHINGTON CO: 11 mi. S. of Hurricane, *F. W. Gould* 1694 (UC). St. George, *A. Eastwood* & *J. T. Howell* 9092 (CAS); *C. C. Parry, M.D.* 41 (Isotype, MO, PH); *M. E. Jones* 11541. Santa Clara Valley, *M. E. Jones* 5138 (POM, UC, MO). Virgin, *A. Eastwood* & *J. T. Howell* 9197 (CAS). Zion Canyon, *M. E. Jones* May 21, 1923 (POM).

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Notes and Discussion

Northern Extension of Zorotypus hubbardi Caudell in Ohio (Zoraptera)

The first Ohio record of *Zorotypus hubbardi* Caudell was reported by Riegel and Koestner (*Amer. Mid. Nat.*, 57 (2):512, April, 1957) from Pike county. This note is to record two additional more northern localities.

On September 20, 1958, two specimens of *Z. hubbardi* were taken at Scioto Trail State Park, Ross county, Ohio (Lat. 39° 13′). The specimens were found at a depth of two inches in a sawdust pile. The sawdust temperature at this depth was 71°F., while the air temperature was 63°F.

On October 12, 1958, two male specimens were taken at a sawmill in Lewisburg, Preble county, Ohio. The insects were collected 18 inches deep on the southeastern side of the sawdust pile. The temperature at this depth was 82°F., and the air temperature was 68°F.

The Lewisburg specimens extend the known range about 40 miles north (approx. Lat. 39° 51′). This record is of interest as it is near the suspected northern limit of the range of this species.

On August 23 and 31, 1958, additional specimens were collected at the original Pike county site. Air temperature on the 31st varied from 76°F. to 82°F. due to rainfall during the collecting period. Temperature of the sawdust was 80°F. at a two-inch depth and 75°F. at a six-inch depth. Zoraptera were found throughout this depth variation.

Three specimens of Enicocephalidae were taken with the Zoraptera. Other collectors have noted that these strange Hemiptera often occur in the same habitat as Zoraptera.—Terrence G. Marsh, Dayton, Ohio, Museum of Natural History.

Book Reviews

THE INVERTEBRATES: SMALLER COELOMATE GROUPS. by Libbie Henrietta Hyman. McGraw-Hill Book Co., Inc., New York. 783 pp., 241 figs. 1959. $13.50.

This, the fifth volume in the series, covers (in individual chapters) the Chaetognatha, Hemichordata, Pogonophora, Phoronida, Ectoprocta, Brachiopoda, and Sipunculida — a seemingly heterogeneous assemblage of invertebrate minor phyla allied because of similarities of coelom, by the possession of a lophophore, or, as in the case of the Sipunculida, because there seems no better place for them. The volume terminates with a chapter entitled "Retrospect" which summarizes recent advances in the particular groups covered in the earlier volumes and expresses recent opinions of the author on such topics as Sedgwick's "Enterocoel Theory" ("fantastic nonsense") and the Protozoa as acellular organisms ("a concept . . . met with the usual resistance of inertia").

To zoologists this volume should be most welcome. In all but the Hemichordata, there have been no synoptic treatments of the groups since before World War II. In fact, these seem to be the first treatments of six of the seven phyla in the English language since before World War I. Here too is the first comprehensive treatment of the Pogonophora. Not only does the volume provide detailed accounts of morphology, physiology, and taxonomy, but also geographic distribution and ecology. Each chapter concludes with a discussion of phylogenetic relationships.

Not being a specialist in any of the groups covered in this volume, I hesitate to criticize the contents. One question, however, did occur to me as I read the vigorous defense of separate status for acorn worms and their relatives as the "Phylum Hemichordata." (This phylum was originally erected by van der Horst in 1939). I don't understand Miss Hyman's assertion (page 74) that "this name does not imply the possession of a notochord by hemichordates; it simply says that hemichordates are 'part chordate', that is, related to chordates, something impossible to deny." Undeniably the two groups are related, but the suffix "chordata" of Hemichordata, Urochordata, and Cephalochordata refers explicitly to the *chorda dorsalis* (notochord). Since the *"Eicheldarm"* of van der Horst is synonymous with the *"stomochorde"* of Dawydoff (1948) and since both of these authors, Miss Hyman, and many other zoologists realize that the structure is probably neither homologous (in the morphological sense) nor analogous to the notochord of the chordates, wouldn't it have been timely to propose a new phylum name for the group which does not contain the root "chord."

It should be noted that the author presently plans to complete volumes VI and VII on the Mollusca and Annelida (and Echiurida) respectively. The Arthropoda (broad sense) are to finish the series. I hope that the invertebrate chordates (*sensu strictu*) are not to be excluded.

The book is well written and well illustrated. Many of the illustrations are original; the remainder, well-chosen. The style one might expect to be dull and pedantic. It isn't. Even those topics which would ordinarily be difficult going, are treated in a lively style. Perhaps the best portions of the book are the discussions of phylogeny: Schizocoela (now replaced by "protostomatous coelomates") and Enterocoela, Protostomia and Deuterostomia, larval similarities and dissimilarities, etc. Needless to say, the author does not avoid controversy. When she does battle, her arguments and comments are based upon thorough knowledge of the literature and firsthand experience — a formidable combination.

In summary, Miss Hyman has produced another valuable and scholarly volume. Biologists in their classrooms and laboratories will continue to benefit from this heroic endeavor.—George R. Bernard, Department of Biology, University of Notre Dame.

FIELD STUDIES OF AMPHIBIANS IN COLOMBIA, SOUTH AMERICA. By Robert C. Stebbins and John R. Hendrickson. University of California Press, Berkeley. 1959. 48 pp., 1 figure in text. $0.85.

Few biologists have had the opportunity to study the life history aspects of neotropical continental amphibians. Aside from several scattered papers and the work of B. Lutz, the bulk of our knowledge is based on fragmentary observations made in the act of collecting material for taxonomic studies. This report is a portion of a broad investigation (sponsored by the Associates in Tropical Biogeography of the University of California) of the breeding behavior of vertebrates in the Magdalena Valley of Colombia. Information has been gathered on one urodele and twenty-five anurans encountered by the authors during a two-months sojourn in the area. The report contains data on variation in morphological characteristics, remarks on the voice, general ecology, sexual dimorphism and reproductive cycles.—Robert E. Gordon, University of Notre Dame.

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Style, arrangement, spelling, and abbreviations should conform to the usage of recent numbers of this journal. Do not underline any words except scientific names. Acknowledgments can be included in the Introduction, or may be offered as a footnote attached to the title of the article. Papers should be concisely written. A subsidy will be required for papers which exceed twenty journal pages in length.

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